Female Relationships and Food Availability in a Forest Community of Chimpanzees.

Kathryn Anne Fawcett

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To my parents,

I hereby declare that:

a) This thesis was composed by myself;

b) The work described is my own work.

Kathryn Anne Fawcett
2nd August, 2000

Abstract

This thesis investigates the behavioural ecology of the Sonso community of chimpanzees, Budongo Forest, Uganda; with particular reference to the social relationships of females. Within both the genus *Pan* and different communities of *P.troglodytes* there is considerable variability in female social relationships. This study quantified both forest food availability and the behavioural patterns of chimpanzees over a 16 month period.

Quantitative measures of food availability were made using a phenology trail including 26 species of known chimpanzee foods. The availability of fruit, leaves, buds and flowers was monitored. Food production was closely linked to rainfall and irradiance levels, revealing 4 distinct seasons. All phenological states were synchronised. The time of highest food production was in March/April, coinciding with the onset of the first annual wet season.

The chimpanzees were observed to alter their behavioural patterns in response to changes in food availability. Party size, in particular the size of all-male and sexual parties, was positively correlated with measures of food availability, but the size of all-female parties did not increase during periods of high food availability. However, the number of females in mixed parties did increase, suggesting a preference for females to associate with males. In addition, the number of oestrous females in the community was positively correlated with measures of food availability. General Linear Models were used to show that food availability was the best predictor of both party size and the number of oestrous females.

The chimpanzees' response to changes in food availability was evident also in their feeding behaviour and activity budgets. During times of resource scarcity the chimpanzees showed a flexible response: either they decreased time spent feeding and fed on lower quality food items, or they increased time spent moving to incorporate seeds and fruit in their diet. Several keystone foods were identified both from phenological data collection and feeding observations. Fruit was the major component of the diet but in contrast to other study communities, young leaves were

also very important. In particular, the young leaves of *Celtis mildbraedii* were not only fed upon during times of low fruit availability but were also a preferred food item at other times.

A bisexual community, with both males and females occupying smaller home ranges within the community range, was revealed by the analysis of ranging behaviour. Male ranges were larger than those of females and within females the most important life history trait determining ranging patterns was their reproductive state: cycling females had larger home ranges. The Sonso community had a relatively small community range, but female core area sizes were similar to those in other communities. Females were identified as being either central or peripheral. There was no obvious relationship between female dominance and ranging behaviour, but there was a tendency for higher ranking adult females to have larger core areas.

Analysis of association patterns showed overall that males were more closely bonded than females. However, some female-female dyads were found to have similar association strengths to those of males. All association indices were greater when food availability was high. The period of transfer between communities was identified as the most important period for females in terms of resource competition.

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Chapter 1

Introduction

This thesis investigates the behavioural ecology of the Sonso community of chimpanzees, Budongo Forest, Uganda; with particular reference to the social relationships of females. This chapter will provide an overview to the general theoretical background of the thesis. More detailed introductions to particular topics will be provided at the start of individual chapters.

The study of behavioural ecology is a synthesis of the disciplines of evolutionary theory, ecology and behaviour. It is concerned with the functional aspect of behaviour. From an evolutionary perspective, behaviours are regarded as the same as any other trait, which may potentially be subject to the process of natural selection. If these behaviours have a genetic basis and affect the fitness of an individual, then they will be subject to selection pressures. Therefore, in long-established environments, the behavioural patterns expressed are likely to produce higher fitness than plausible behavioural alternatives (Sibly & Smith, 1985). Behavioural patterns which are the products of evolutionary selection pressures on individual fitness, and therefore have an adaptive or functional significance, are termed *strategies* (Strier, 2000). These include feeding strategies for obtaining food, life history strategies which are the patterns of gestation, development and maturity, and reproductive strategies which are behaviours that increase the likelihood of an individual gaining access to mates. During evolution, natural selection will favour individuals who adopt a suite of strategies which will maximise their gene contribution to future generations. The strategies that individuals adopt will depend on the influencing factors of ecology, competition and predation. Selection will result in individuals who are most efficient in the strategies they pursue. What is 'optimal' will depend upon the alternatives available, which will depend upon various constraints imposed by phylogeny, physiology and ecology (Krebs & Davies, 1993). The social organisation or social structure of a group may be considered as the

outcome of individual strategies. Where these strategies are best formed in association with other individuals, groups will form (van Schaik & van Hoof, 1983). This thesis is concerned with the ecological influences of food distribution and availability on the grouping, feeding and association strategies of individuals in a community of forest dwelling chimpanzees.

Wrangham (1980) first proposed a model of the evolution of social organisation in female-bonded primate groups which emphasised the central importance of female relationships. The model uses the principle that, primarily, it is the selection pressures on the behavioural responses of females to food distribution, which ultimately determine social systems. The reproductive success of females is assumed to be primarily limited by the rate at which they can raise offspring, and therefore access to food resources is most important; whereas the reproductive success of males is thought to be constrained by sexual opportunities, i.e. access to females. Wrangham (1980) suggested that when feeding sites are in discrete and defensible patches, individual females should cooperate to defend food patches against other groups. The costs incurred by feeding competition between group members would be outweighed by the benefit of cooperation between group members against other groups. During times of food scarcity these species should switch from a diet of high-quality food dispersed in discrete patches to a uniformly distributed low quality food, in order to maintain group cohesion. However, it may not be necessary for all species to modify their diet as long as the benefits of cooperation remain profitable (Barton & Whiten, 1993). Individuals are assumed to preferentially cooperate with kin relations resulting in the formation of female-bonded groups. Thus, from the model, frugivores are expected to form female-bonded groups of kin members, whereas female cooperation should be less important in folivores, and thus female relationships be less differentiated. Van Schaik (1989) extended this model to include predation as an important reason why species should form groups. In addition, he emphasised the importance of within-group competition as well as between-group competition in shaping social organisation. He distinguished two types of competition; scramble and contest. These extensions to the model allowed the model to be applied to female and non-female-bonded groups.

Isbell (1991) analysed feeding competition between different primate species and concluded that the food distribution i.e. clumped or dispersed, influences the type of intra-group competition, whereas food abundance influences inter-group competition. This was due to the observation that despite the form of intra-group competition groups may still compete with neighbouring groups for access to food. Sterck et al. (1997) expanded the model again to include the social factor of male coercion and infanticide risk and the effects of habitat saturation (Sterck, 1998).

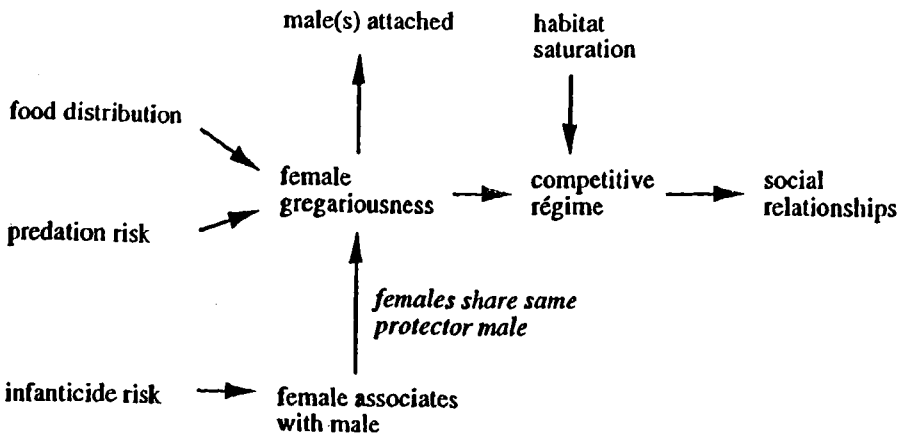
Thus, it is the nature of female competition which is important for shaping the social organisation of primate groups. Sterck et al. (1997) distinguished three features which describe the character of female agonistic relationships. Dominance behaviour may be either egalitarian or despotic or somewhere along a continuum. Within despotic societies the dominance relationships may be formalised by formal acceptance of subordinance, the dominance hierarchy may show linearity and coalitions may exist between individual females which may be either kin or non-kin based. These dominance hierarchies may in turn be based upon individual relationships (individualistic) or kinship (nepotistic). In addition, the degree to which these relationships are pursued may differ to include the effects of tolerance.

The type of feeding competition experienced will be determined by the size and distribution of food resources (Bradbury & Vehrencamp, 1976; van Schaik, 1989; van Hoof & van Schaik, 1991; Isbell, 1991). Where *scramble* competition predominates, a dominance hierarchy will not be evident, thus individuals within a group will receive similar access to food resources. Scramble competition may be reflected as adjustments of day ranges or home range size to group size (van Schaik & van Noordwijk, 1988; Janson & Goldsmith 1995) or shorter patch residence times or lower foraging efficiency in larger groups (Utami et al.,1997). *Contest* competition involves agonistic interactions and where strong, will lead to a combination of formalised dominance hierarchies, long-term alliances with kin or non-kin and female philopatry (Janson, 1988; Barton & Whiten, 1993; Saito, 1996). In reality, groups will experience a mixture of contest and scramble competition. It is the intensity of contest competition which generally appears the most important in shaping social organisation. Here follows is an outline of how the extent of contest

competition within- (WGC) and between-groups (BGC) may affect female relationships (summarised from Sterck, 1997). Where WGC and the ecological cost of dispersal, e.g. predation risk or inefficient foraging associated with the transfer period, are low, females may be expected to transfer between groups. When WGC is high, females may only transfer between groups in association with kin-related alliances, i.e. group fission. When WGC is weak formal dominance hierarchies and alliances are not expected because they will not increase the likelihood of an individual gaining access to food. Individual females are able to transfer between communities because they do not lose their coalition partners, and should also face little or no competition when joining a new group. In theory, BGC may occur with either weak or strong WGC. If BGC is strong and WGC is weak, within group hierarchies and coalitions are unnecessary; however, females are expected to live in kin-related groups in order to ensure the participation of all group members in group defence. Where BGC and WGC are both strong, females should display formalised dominance hierarchies, coalitionary support and female residence. However, high ranking females may be expected to show *tolerance* towards lower ranking females, i.e. allowing them access to food resources or social partners, in order that the higher ranking females maintain the support of lower ranking females in BGC situations. In addition to these factors Sterck (1997) proposes two other possible influences on female relationships. Firstly, habitat fragmentation, as a result of human disturbance, may lead to an increased density of primates and thus *habitat saturation*. Under such situations, female relationships which would usually be egalitarian may become despotic and in extreme cases this may lead to the eviction of female members. Another social factor which may influence female social relationships is that of male coercion and infanticide avoidance. Females may benefit from male protection against infanticidal males of other groups. In this scenario, the primary reason for females to live in a group is the protection offered by male(s), rather than the risk of predation or defence of food resources. Support for the model has come from comparisons of the differing social organisation between closely related species, constrained by the same phylogenetic traits, or the same species in different

environments, (Barton et al., 1996; Koenig et al., 1998); and from studies of sympatric species (Sterck & Steenbeck, 1997).

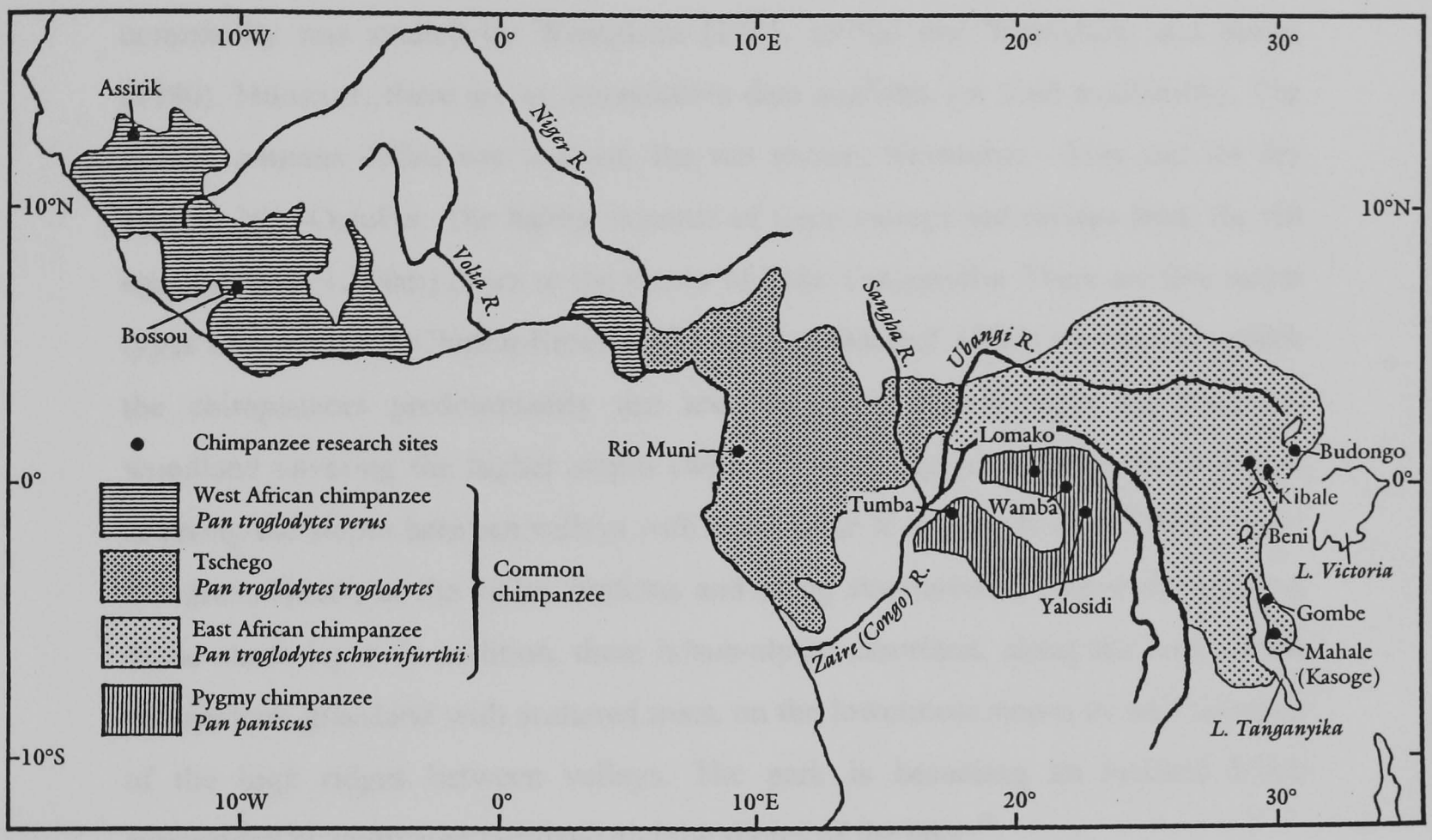
Fig 1.1 Socioecological Model of the Influences of Food Distribution, Predation Risk, Infanticide Risk and Habitat Saturation on the Evolution of Female Competitive Regimes and Ultimately Group Social Organisation (from Sterck, 1997).



Chimpanzees exhibit a fission-fusion society, the size and composition of temporary smaller parties within the community continually changing depending upon the availability of resources and on individual relationships (Fleagle, 1999). They are therefore a useful model for testing the predictions of evolutionary models of social organisation. The fission-fusion social organisation is thought to be a response to a highly dispersed food source and the resulting feeding competition (Wrangham, 1979a; Dunbar, 1988). Chimpanzees have a predominantly frugivorous diet supplemented with leaves and insects. The cost of scramble competition probably prohibits the formation of larger groups and the fission-fusion system allows a flexible grouping response to food availability and adaptation to life history variables. The fact that females do not cooperate to gain access to fruiting trees suggests that the nature of their subsistence diet during periods of food scarcity, forces females to forage alone (Wrangham, 1979a, 1980). Studies from captivity and the wild have shown wide variation in the nature of chimpanzee female social relationships. However, so far few studies have quantitative data on the ecological variables which are predicted to influence these relationships. This thesis will address the influence of ecological variables on the social relationships of the Sonso

chimpanzee community and, where appropriate, make comparisons with the social relationships of other chimpanzee communities. A description follows of the location, habitat and years of study of the main communities to which the results from this study are compared.

Fig 1.2 The Distribution Of Chimpanzee Species (adapted from Kano, 1992).



Chimpanzees have a wide distribution, ranging across equatorial Africa from the West African coast to the forest/savanna zone in East Africa. There are two species of chimpanzees *Pan troglodytes* and *P. paniscus*. In addition, there are three sub-species of *P. troglodytes; P. t. schweinfurthii, P. t. troglodytes, P. t. versus*. Fig 1.2 shows the distribution of these species and the location of the major study sites.

Gombe:

The Gombe National Park is towards the eastern extreme of the chimpanzee distribution range. Field observations started in 1960 and have continued until the

present day (Goodall, 1968, 1986). This long-term study has offered valuable insights into chimpanzee behaviour. Now, as observations on second and third generation individuals in the community become available, it is possible to assess the adaptive significance of this behaviour (Pusey et al., 1997). Early observations were aided by the provisioning of the chimpanzees with bananas at the research station: where the majority of early behavioural observations were made. Provisioning continues today at a much lower frequency. The behavioural ecology of this community was studied by Wrangham (1975, 1979a) and Wrangham and Smuts (1980). However, there are no quantitative data available on food availability. The rainfall patterns define two seasons; the wet season, November - May and the dry season, June-October. The habitat consists of steep valleys and ravines from the rift escarpment (+1,500m) down to the shores of Lake Tanganyika. There are five major types of vegetation (Clutton-Brock, 1972 cited in Goodall 1986): the habitats which the chimpanzees predominantly use are; the open *Brachystegia* (or miombo) woodland covering the higher slopes (with no shrub layer); semideciduous forest, covering the slopes between valleys with a moderate to extremely dense shrub layer; evergreen forest, in the valley bottoms and along stream-beds, with a moderate to dense shrub layer. In addition, there is sub-alpine moorland, along the crest of the escarpment; grassland with scattered trees, on the lowermost slopes as well as many of the high ridges between valleys. The park is becoming an isolated block surrounded by cultivated farmland and the shores of the lake.

Mahale:

Studies began here in 1965 and continue to the present day. Again, the habituation of the chimpanzees was aided by provisioning (sugar cane). Nishida (1990) describes semi-deciduous or semi-evergreen gallery forest as the most important habitat for chimpanzees which occurs at altitudes between 780 and 1,300m. *Brachystegia* woodland is also present and is the major habitat in the study area. At higher altitudes there is high-altitude montane savanna and stands of bamboo. The chimpanzee studies have centred on social behaviour (Nishida, 1968, 1990) and no quantitative

data on food availability exist. The climatic seasons are presumed to be similar to those at Gombe, but humidity is higher (Boesch & Boesch-Achermann, 2000).

Bossou:

The research at this study site has mainly focused on tool-use behaviour, and there have been frequent, but not continual, observations since 1976. This small community lives in an extremely disturbed habitat, isolated from other communities by surrounding farmland and villages. Thus, demographic features of this community may be atypical (Sugiyama & Koman, 1979; Sugiyama, 1999).

Tai:

This study was initiated in 1976 and has had continual observations since 1979. Provisioning was not used to accelerate the habituation process. There are two rainy seasons, March - July and September-November, but no clearly defined dry season. The study site receives an annual rainfall of approximately 1800mm. Detailed ecological data of the study area are not available, but based on rainfall patterns the forest is regarded as experiencing less seasonal variation in productivity than the East African forest study sites. Tree species of evergreen and semi-deciduous forest overlap (Boesch & Boesch-Achermann, 2000). Observations have focused on tool-use and hunting behaviour and more recently behavioural ecology, yet detailed ecology and food availability data are lacking.

Kibale:

This is geographically the closest long-term study site to Budongo Forest. Studies of chimpanzees were initiated by Ghiglieri (1984) at the Ngogo study site. Later chimpanzee studies were continued by Isabirye-Basuta (1988) and Wrangham et al. (1992, 1996) at the Kanyawara study site. Recently Watts (1998), has started to habituate and take behavioural observations of the Ngogo community. There is a bimodal distribution of rain: May - August and December - February tend to be drier than other months, with the May - August period being the longest dry season. Mean annual rainfall is approximately 1600m. The forest is classified as *Parinari* forest

and the terrain is undulating. Kanyawara is at an elevation of 1500m and Ngogo is approximately 150m lower. The vegetation at Kanyawara is a mosaic of mid-altitude moist forest, secondary forest, tall grasslands, swamps and softwood plantations (Wrangham et al., 1991). The habitat at Ngogo is similar without the plantations or logged forest. There are detailed phenological records of food availability at this site. There are differences in tree species composition and phenology patterns between the two study sites, which are 10-15 km apart.

Thus, in summary, habituated communities of chimpanzees have been studied in a broad range of ecological habitats; from the relatively dry, seasonal and mosaic habitats of Gombe and Mahale, to the still seasonal but more contiguous forest habitat of Kibale, to the wetter and less seasonal forest environment at Tai.

Aims

This thesis will address issues of behavioural ecology, in the Sonso community of chimpanzees, Budongo Forest, Uganda. Quantitative data will be collected on both food resources and the behavioural responses of the chimpanzees to changes in food availability. Female relationships are highlighted through differences in sex and life history strategies. The following aims will be investigated.

- Examine the phenological patterns of Budongo Forest in order to assess fluctuations in food availability for the chimpanzee community. Investigate the underlying climatic variables which are influencing the phenological patterns.
- Investigate the relationships between changes in food availability and chimpanzee grouping patterns and the additional covariant of the availability of oestrous females.
- Quantify the chimpanzee diet and any changes in diet or activity patterns in responses to periods of food scarcity. Possible keystone foods will be highlighted.
- In order to address questions of community membership and to aid the understanding of association patterns within the community, individual and community ranging patterns will be analysed.
- The importance of female dominance and female associations will be addressed. In particular, the possible benefits of female high rank will be discussed and the response of female association patterns to changes in food availability.

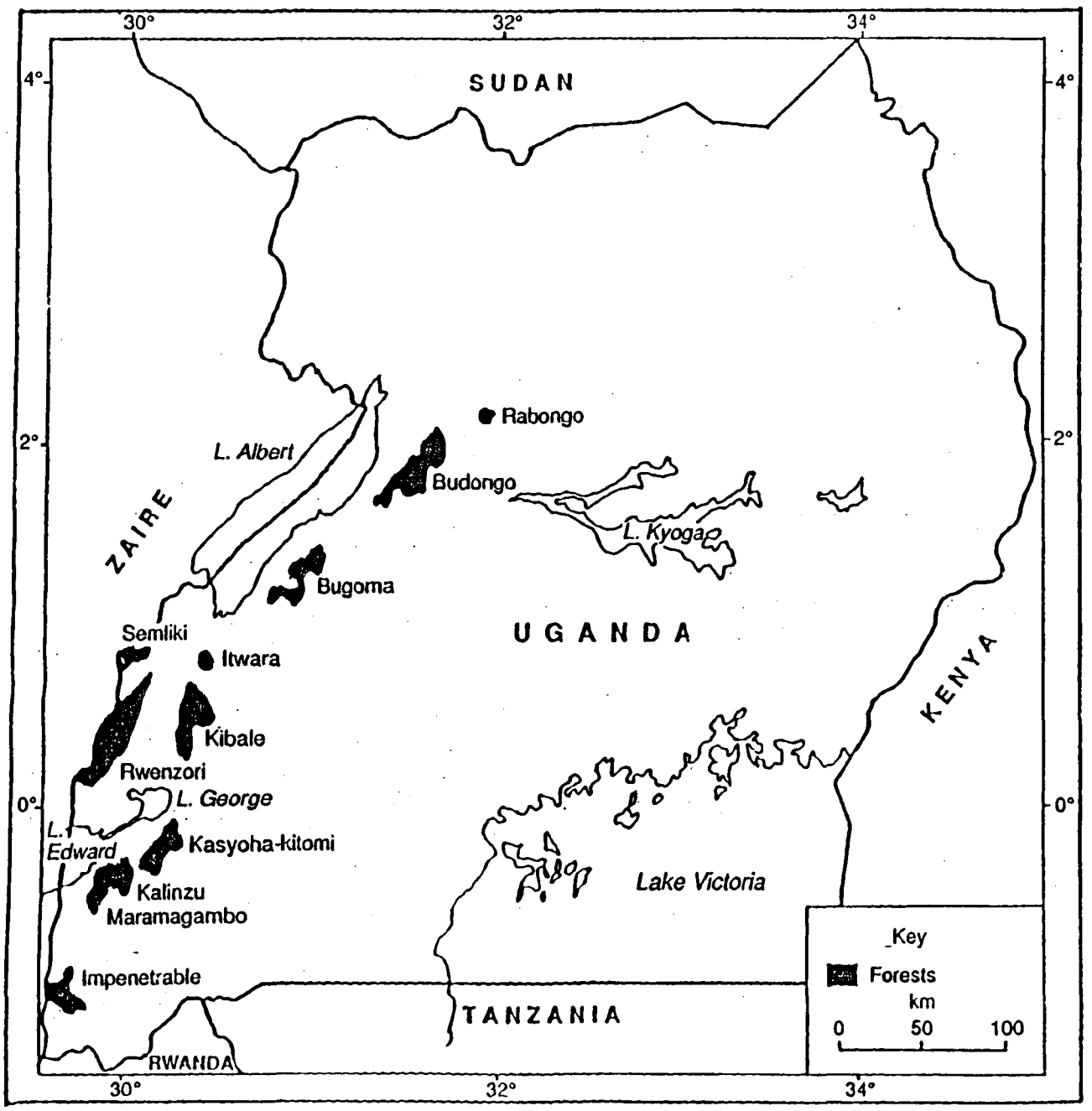
Chapter 2

The Study Site and The Sonso Chimpanzee Community.

2.1 Location

The Budongo Forest Reserve is situated in the west of Uganda, (latitude $1^0$37'-$2^0$00'N; longitude 31^0 22'-$31^0$6'E) , east of the Western Rift Valley escarpment and Lake Albert, within in the districts of Masindi and Hoima.

Fig 2.1 Location Of The Budongo Forest Reserve And Other Natural Forests Containing Chimpanzees In Uganda. (from Reynolds, 1992)



The forest lies at an average altitude of 1100m (3600ft) (min. 750m, max. 1250m) above sea level. The terrain is gently undulating with a gradual slope NNW towards the Albertine escarpment. It covers an area of 793km^2 of which 428km^2 (53%) is continuous forest cover, the remaining 47% comprises grassland communities thought capable of supporting forest (Howard et al., 1997). The reserve is, in part, contiguous with the Murchisson Falls National Park and the Bugungu and Karuma Game Reserves.

2.2 Climatic Variables.

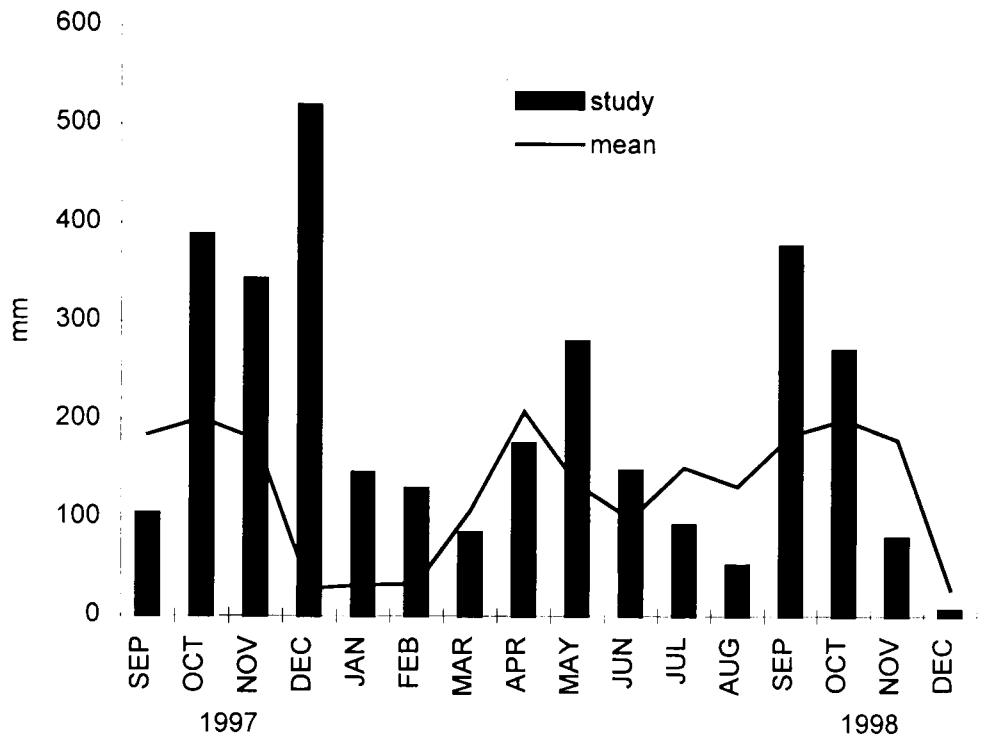
Rainfall

Budongo has a bi-modal distribution of rain with a mean annual rainfall of around 1600mm, (range from 6 years of data =1240.7-2187.3mm) (see Fig 2.1). The most distinctive pattern is the severity of the dry period in or around January. This has been observed in every year so far, except 1998. During October, November, and December 1997 and January and February 1998, the amount of rainfall was consistently greater by at least 20% than all previously recorded months, since the beginning of data collection in 1993. This was most likely due to the world-wide effects of El nino. In some years, there is also a shorter and less severe period of *drought* at sometime during the period June to August. The precise timing and duration of this dry period, if it does indeed occur, varies from year to year resulting in a blurring on the graph of average rainfall.

Table 2.1 Rainfall(Mm) From 1993-1998 And Average (av.) Collected By The Budongo Forest Project Field Station, Sonso, Budongo Forest.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
93	7.6	79.4	91.6	132.3	140.1	131.5	113.2	112.4	151.1	111.2	130.2	40.1	1240.7
94	8.6	0.6	80.7	153.1	195.0	55.2	192.2	185.0	210.1	241.8	252.0	26.2	1600.5
95	2.8	7.0	100.8	222.4	143.7	109.9	197.2	72.1	155.2	238.8	166.4	44.1	1460.4
96	51.0	76.6	184.7	256.0	134.5	101.7	103.1	219.7	223.9	212.5	172.6	0.0	1736.3
97	86.6	0.0	81.8	282.1	58.5	97.1	151.9	72.0	104.2	388.6	343.8	520.7	2187.3
98	146.0	130.0	84.3	176.0	281.0	148.0	92.7	51.4	378.0	272.0	80.1	6.0	1845.5
av.	50.4	48.91	104	203.7	158.8	107.2	141.7	118.8	203.8	244.6	190.9	106.2	1678.5

Fig 2.2 Comparison of Rainfall Each Month During This Study (Bars) and The Average Rainfall From Previous Years data, (1993-1996/7), (Line).



The rainfall patterns in each year are similar, even if the actual amount of rainfall varies, Kendall Coeficient of Concordance R = 34.410, N=6, $p<0.01$. Based on climatic data, Richards (1996) classified Budongo Forest as tropical wet seasonal. General climatic characteristics of this forest type are 1) a monthly mean temperature of at least 18°C. 2) annual rainfall of at least 1700mm (and usually above 2000mm). 3) no dry season or a short one of fewer than four consecutive months with less than 100mm rainfall. Table 2.2 shows the rainfall patterns and associated seasons for the duration of this study.

Table 2.2 Rainfall Patterns And Associated Seasons During This Study.

Year	Starting month	Ending month	Season
1997	August	September	Dry season 2
1997	October	December	Rainy season 2
1998	January	March	Dry season 1
1998	April	June	Rainy season 1
1998	July	August	Dry season 2
1998	September	October	Rainy season 2
1998	November	December	Dry season 1

Temperature

Temperature and rainfall variables were plotted on a single graph to produce a climate diagram according to Richards (1996) for the period before this study (Fig 2.3) and for the period of this study (Fig 2.4). The temperature scale (0-50 degrees C) is twice the scale of that of rainfall (0-100mm). To save space the rainfall scale above 100mm is reduced by a factor of 10. From this diagram three types of months are distinguished; ***wet:*** rainfall exceeds 100mm (taken as a rough guide to potential evaporation in the tropics); ***drought***: months in which rainfall falls below that of temperature; ***dry*** or ***intermediate***; months when rainfall falls beneath 100mm but not beneath that of the temperature graph. Using average figures for data collected between 1993 and 1997, (Fig 2.3), Budongo Forest experiences drought months during December - February and can be classified as wet for the rest of the year, except in June, the average rainfall is 99.08mm. As already stated the timing of the second period of rainfall is variable from year to year. A climate diagram was then produced for the duration of the study period (Fig 2.4). This showed the absence or delay of the characteristic drought period between December 1997 and February 1998. However, a period of drought was evident the following year. An uncharacteristic dry or intermediate period occurred during March 1998. This perhaps represented a delay in the usual drought between December and February. The climatic patterns appear to have settled back to normal patterns by July 1998, with the usual dry or intermediate period.

Other Climatic Variables

Comparing the rainfall data from Budongo with climatic data collected from a weather station in Kampala, Budongo was found to have a similar rainfall pattern. Therefore data on other climatic variables collected in Kampala were used to define the characteristics of the four seasons in Budongo (see Table 2.3).

Fig 2.3 Climate Diagram For Average Data Before Study Period (1993-1997)

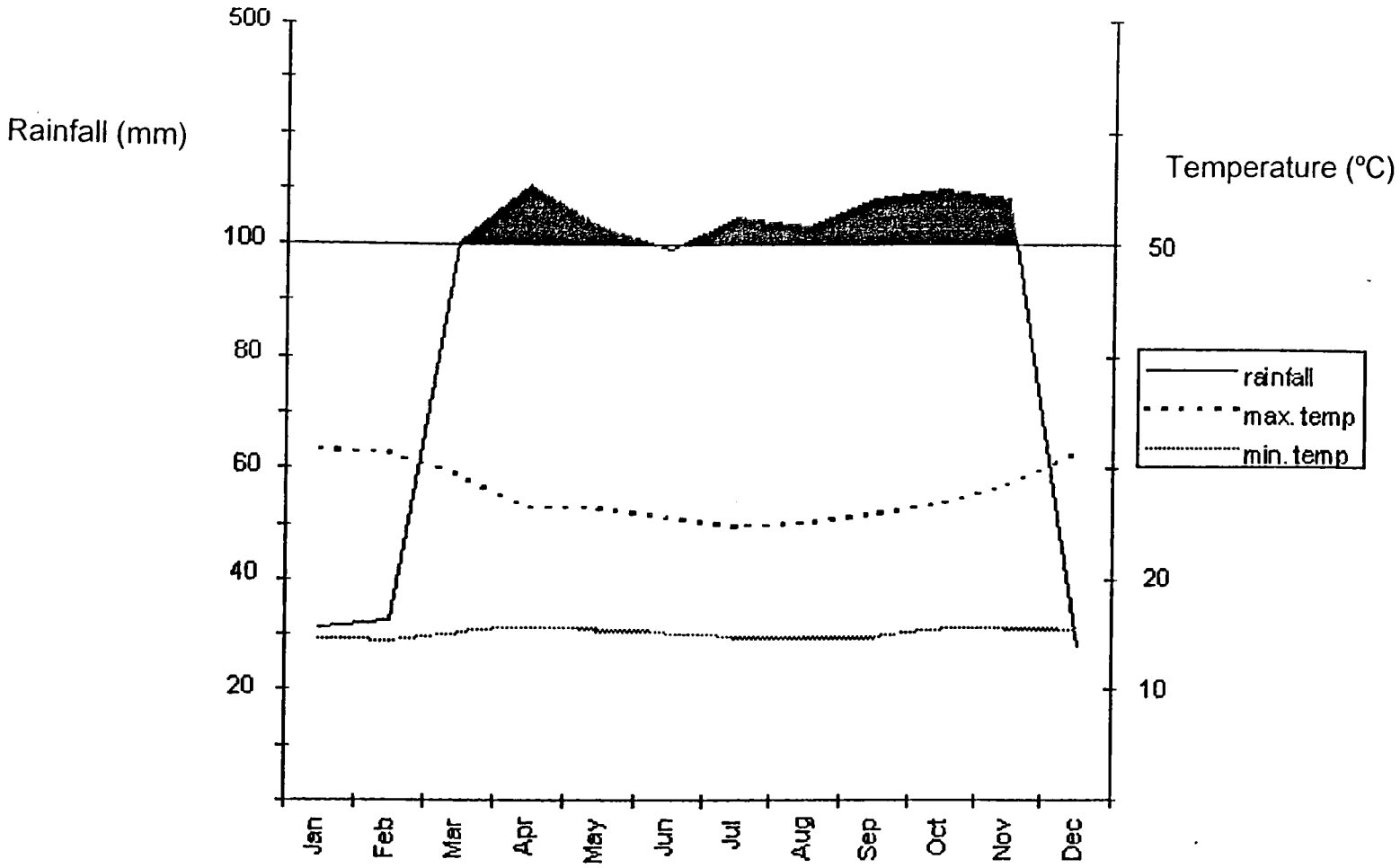


Fig 2.4 Climate Diagram For This Study Period

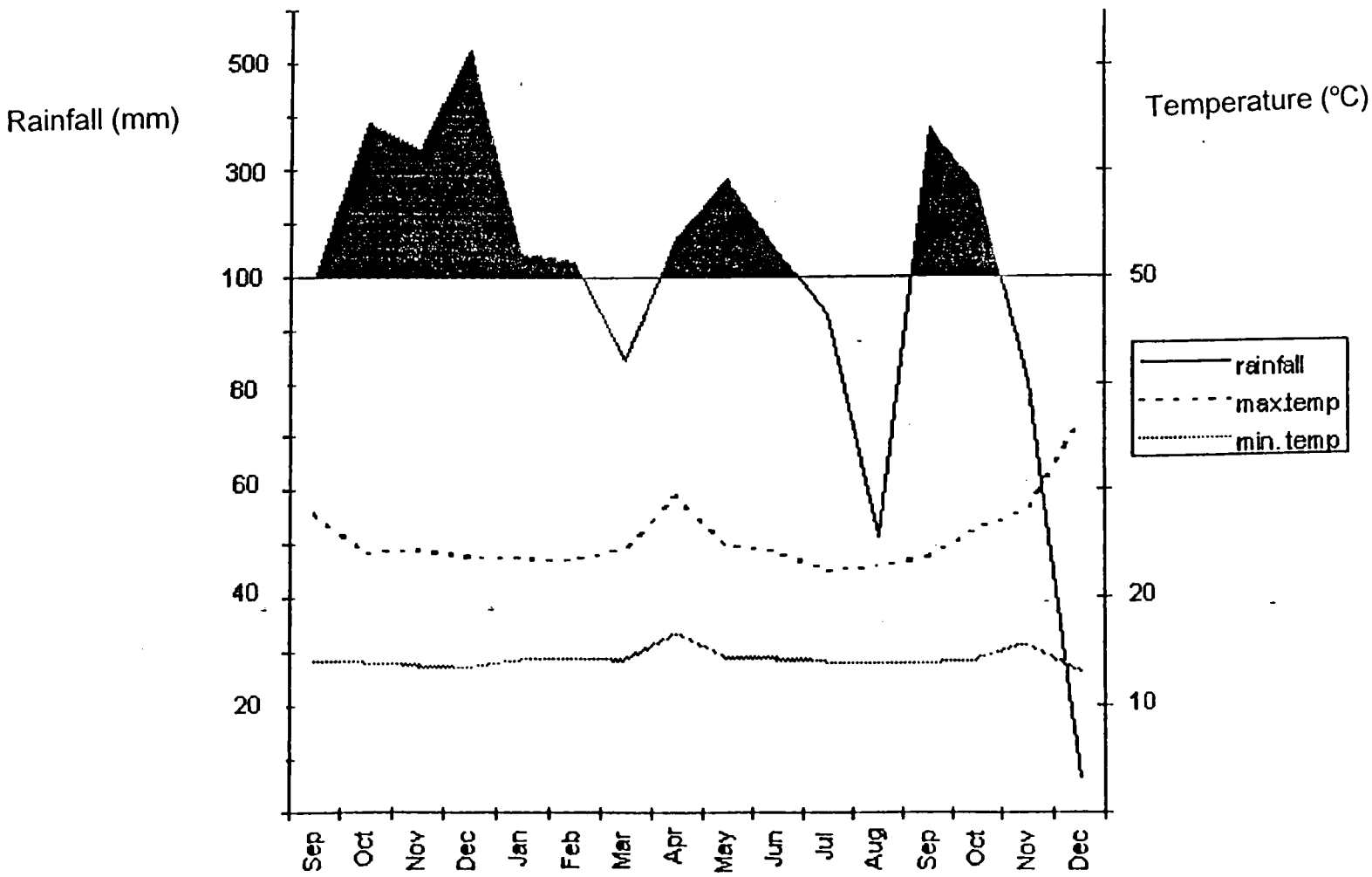


Table 2.3 Summary Of Climatic Data From Kampala Weather Station.

Climatic Variable	Month
Maximum Temperature	January
Minimum Temperature	August
Maximum Humidity	August (0900), May (1500)
Minimum Humidity	January (0900), Jan (1500)
Maximum Cloud Cover	April, May
Minimum Cloud Cover	January, August, September, December
Maximum Hours of Sunshine	January
Minimum Hours of Sunshine	July

Characteristics Of The Seasons.

The first dry season of each year, (Dry season 1), which occurs sometime during the months of December to February is characterised by having the lowest rainfall; the maximum average daily temperature, the minimum relative humidity average, the minimum cloud cover at both 0830hrs and 1430hrs and the maximum hours of sunshine. The second dry season of each year, (Dry season 2), which occurs between June and August and is usually referred to as a minor dry season, is characterised by having reduced rainfall, the minimum average daily temperature, the maximum relative humidity average, the minimum cloud cover at 0830 hours only, and the minimum average hours of sunshine. Therefore the two dry seasons although both being periods of reduced rainfall, do not only differ in respect to all other climatic variables, they are also characterised as displaying values at opposite extremes of all other variables. Thus, Budongo may be considered as experiencing *four* seasons.

The two rainy seasons fall in between the two dry seasons and appear to exhibit moderate climatic variables, with the obvious exception of rainfall, compared to the extreme variables of the two dry seasons. The differing characteristics of the two dry seasons are important. If, classifying the climatic patterns of Budongo Forest by rainfall alone we would describe the seasons as bi-modal. However, on closer examination the seasons may be characterised as dry season 1, followed by a wet season, followed by dry season 2, followed by another wet season. This has important implications for the vegetation and primary consumers of the forest as will be discussed in Chapter 4.

2.3 Vegetation

Budongo forest may be considered as an isolated fragment of the vast Central African forest block. The flora is representative of other mono-dominant forests in The Democratic Republic of Congo and also of other East African forests. Until this century, it had minimal contact with human populations and favourable climatic conditions in the past have lead to a natural expansion of Budongo. The only pre-colonial restraints on the forest expansion were savanna fires and elephants (Paterson, 1991). Howard (1991) argued that Budongo Forest was probably the most important in Uganda for tree species conservation. The reserve alone contains 37% (465 sp.) of all Uganda's known tree and shrub species.

The forest has been classified by Eggeling (1947), as typical lowland rain forest, then later by Langdale-Brown et al. (1964), as medium altitude moist semi-deciduous forest. Nearly all of the larger canopy species are deciduous, a notable exception being *Cynometra alexandri*, shedding leaves during the December - February dry season. The vegetation communities have been studied in detail by Eggeling (1947) and Synott (1985). Eggeling (1947) proposed four main forest types, three of which follow an ecological succession (see Fig 2.5). Subsequent monitoring of long term plots established by Eggeling, (Sheil, 1996), and the use of aerial photographs (Plumptre, 1996) partially support this idea.

Forest Types according to Eggeling (1947):

Colonising forest: This forest type occurs along the forest edges. Two types can be distinguished; Maesopsis forest and Woodland forest. Each type is maintained for one generation and then develops into mixed forest. Termite mounds are characteristic within the younger forest.

Mixed Forest: This forest type is characterised by a rich and diverse species composition. Almost 50 species are recognised. There is no single canopy dominant species. This forest type covers much of the forest and contains the valuable timber trees. The proportion of *Cynometra alexandri* present depends upon the stage in succession.

Fig 2.5 Map Of Budongo Forest Showing Different Vegetation Types

Cynometra forest: This is considered to be the climax vegetation. This forest type is overwhelmingly dominated by *Cynometra alexandri* with a scarce understorey of small trees and shrubs. (*Lasiodiscus mildbraedii*, or with a mixture of *Strychnos mitis, Alstonia boonei, Celtis wightii, C. zenkeri.*)

Swamp Forest Confined to areas around streams and seasonally waterlogged areas. It is considered to be an edaphic climax. It is the least common forest type and the most structurally diverse with many climbers. Contains patches of *Raphia farinfera*, and scattered *Pseudospondias microcarpa.*

A distinguishing feature of Budongo Forest is the mono-dominance of *C. alexandri* in the climax forest. Eggeling (1947) proposed that *C. alexandri* is a superior competitor for light and nutrients within certain climatic regimes. Osmaston (1959) working in Bugoma Forest proposed that *C. alexandri* trees became dominant on poor clay soils whilst mixed forest was capable of maintaining itself on richer soils. This idea was supported by Langdale-Brown et al. (1964). A further suggestion is that elephants (once very abundant in Budongo) do not debark *C. alexandri* to the same extent as other species resulting in an elephant induced deflected climax forest (Laws et al. 1975; Plumptre et al. 1997).

2.4 History of Forest Management

The Budongo Forest reserve is the largest and most valuable timber forest in Uganda (Howard, 1991). Timber has been extracted from the forest since around 1910. Initially at low levels, then in the 1930's the reserve was gazetted by the British Colonial Administration and working plans were drawn up for the sustainable extraction of timber, essentially 4 species of mahogany and 3 species of *Entandrophragma*, for both domestic and international markets (Plumptre et al., 1997; Paterson, 1991). Management of the forest continued after the end of British administration by the Uganda Forest Department. Detailed management records of each compartment have been kept and research plots monitored (Plumptre, 1996), (see Fig 2.6). Initially, in the 1930's it was intended to set up a system of polycyclic felling every 40 years, felling trees with DBH greater than 1.3m. In the fifties research showed that regeneration was slower than expected. Plans were then altered

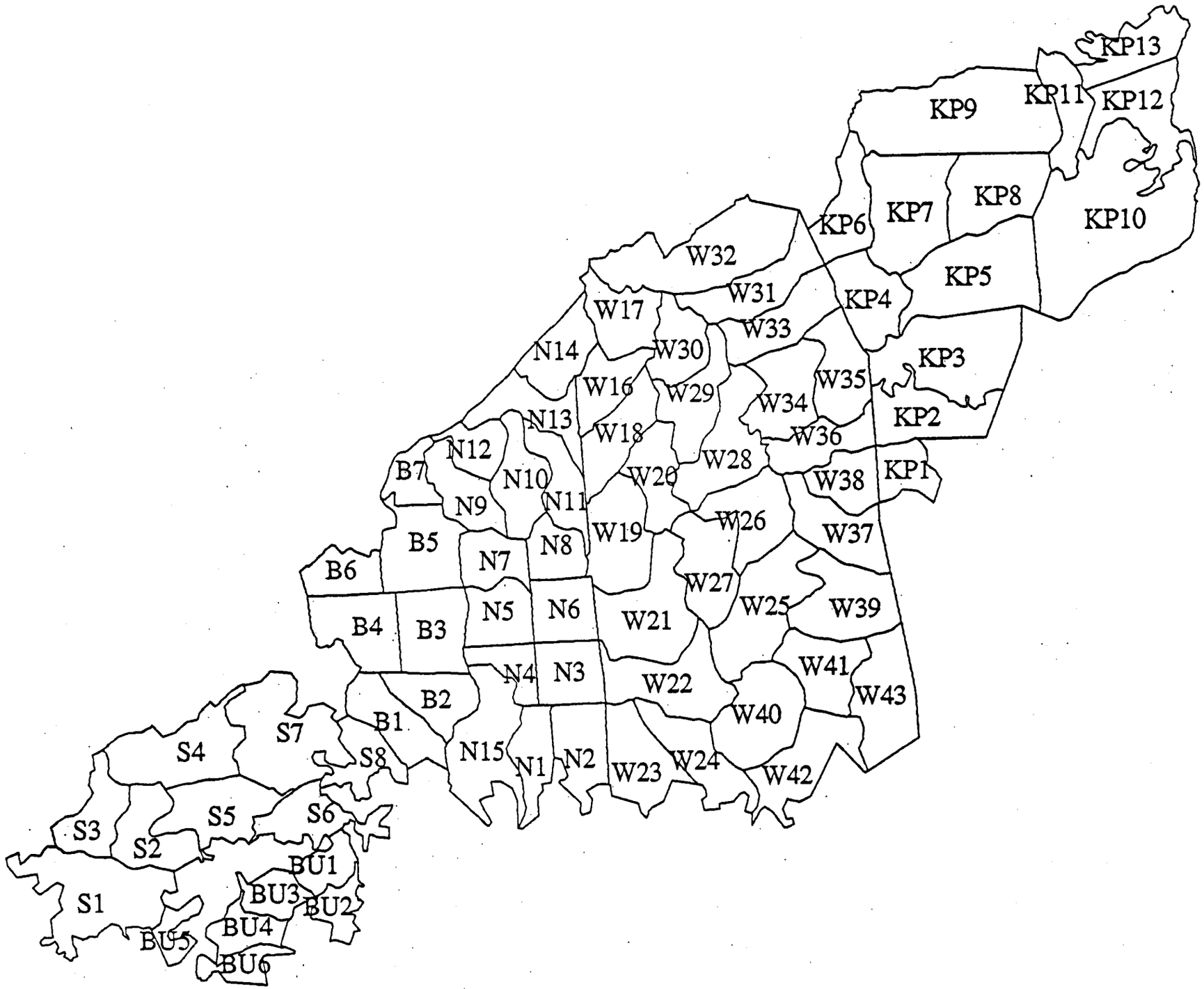


Fig 2.6 Map Showing The Different Compartment Numbers Of Budongo Forest

to a monocyclic system, felling every 80 years and the critical DBH value was reduced to 75cm. Replanting of mahoganies (*Khaya* and *Entandrophragma*) was carried out to encourage regeneration. This practice was later stopped when research revealed that replanting did not accelerate the regeneration process. Also during the 1950's and 1960's arborocide treatment (2,4,5-T and 2,4-D in 1:2 proportions and mixed with diesel) was applied to various 'weed' species of tree i.e. trees with no marketable value, in particular to *Cynometra alexandri* (the dominant canopy species). The aim was to open up the canopy and encourage the spread of mixed forest. This treatment stopped in the 1970's when more species of trees became marketable and when it also became more difficult to import the chemicals. During the Ugandan civil war and the period shortly thereafter, illegal pit-sawing (previous logging had been selective mechanised logging) by local communities began. This problem persists until the present day.

The Ugandan Forestry Department now manages the forest from a largely pit-sawing perspective. Very little mechanised logging is currently in practise. The forestry department monitors and assesses the amount of timber to be felled from a compartment and then sells the licences for trees to be cut. Problems arise as the forestry department does not have the men or resources to adequately patrol the whole forest. Another practical problem, with the exception of the nature reserve, is that on the ground in the forest it is very difficult to judge where one compartment ends and another begins. This makes it easy for encroachment into the forest from compartments designated for pit-sawing. A community forestry initiative is under discussion, the aim to give the local communities increased involvement in the management and profits of the reserve. However, caution is needed to introduce such a programme to the communities now living around the Budongo Forest Reserve. This is because the communities are largely transient in nature, having moved into this area from less politically stable areas of Uganda, Sudan and the Democratic Republic of Congo, often attracted by the income generating opportunities in the forest. In addition, traditionally, Bunyoro people do not have an association with the forest, rather they are connected to the savanna surrounding the forest (Paterson, 1991)

Comparative analyses of the biodiversity of all forests in Uganda included Budongo in a list of 11 forests to be designated as a strict nature reserve, SNR, as part of a national project undertaken by the Ugandan forestry department (Howard et al. 1997). In addition to the exceptionally rich fauna and flora, Budongo is situated at elevations not otherwise represented in the existing national parks. The SNR will be designated as a centrally located core area, with increasingly intensive resource use permitted towards the periphery of the reserve, thus satisfying multiple-use management objectives. The Budongo Forest Project has been working in close association with the Forestry Department to draw up management plans for the future. One benefit of this association is the designation of the compartment which includes much of the research area as an SSSI (Site of Special Scientific Interest). This means that no further logging will occur in this area in this compartment.

The forest compartments within which the Sonso community of chimpanzees habitually range are N1, N2, N3, N4, N15. See table 2.4 for a summary of the compartments logging history and vegetation types.

Table 2.4 Summary of Forest Compartments and Types within the Sonso Chimpanzee Community Range.

	N1	N2	N3	N4	N15
Logging Dates	1945	1945/47	1947/52	1952/54	unlogged
Forest Types	mixed swamp	mixed swamp	mixed colonising	mixed swamp	Cynometra

2.5 The Fauna of the Budongo Forest Reserve.

The fauna of Budongo Forest, as with the flora, is representative of a sub-section of the communities which have colonised this outlying forest block from the central African, Congo basin. In the past there were substantial populations of buffalo, (*Synceros caffer)*, and elephants, (*Loxodonta africana africana)*, entering the forest from the savanna to the north. However, as a result of high levels of poaching during the civil war these populations are now devastated. Lions have been reported from the northern boundary. However, neither lions nor leopards are considered a serious predation threat for the Sonso chimpanzee community. Other primate species present

are Black and White colobus, *(Colobus guereza)*, Red tailed Guenons, (*Cercopithecus ascanius)*, Blue monkeys, (*Cercopithecus mitis)*, Baboons, (*Papio anubis)*, and the potto, (*Perodicticus potto)*. No bush babies have been reported but it would be surprising if they were not present. The noisiest inhabitant is the little studied tree hyrax, *Dendrohyrax arboreus*, which could potentially compete with any bush babies. Duikers, *Cephalophus rufilatus*, red, and *Cephalophus monticola* blue, bush buck, *Tragelaphus scriptus*, bush pigs, *Potamochoerus porcus*, and guinea fowl, *Guttera edouardi*, name are frequently hunted by local human populations. None of the primates are actively hunted. It is not in the tradition of the Bunyoro community to hunt and eat primates. However, this situation could change with the increasing immigration of people from the Democratic Republic of Congo. Many of the chimpanzees have snare injuries and evidence during this study suggests at least one individual may have died as the result of a snare injury (a skeleton of a chimpanzee from another community, was found with a snare attached). During the late 1980's there was evidence of a trade involving capturing infant chimpanzees for export.

Budongo forest has many locally endemic bird species including the rare and endangered Nahlin's francolin which is currently under study.

The result of management practices has been an increase in the percentage area of mixed forest, which has benefited many frugivorous species (Plumptre & Reynolds 1994). Plumptre and Reynolds (1994) compared primate densities, using line transect techniques, in eight forest compartments, two of which had never been logged and 6 which had been logged at approximately 10 year intervals since 1940. They concluded that *Colobus. guereza, Cercopithecus. mitis* and *Cercopithecus. ascanius* have all benefited from the logging practises in Budongo and that logging has had little or no detectable effect on the density of chimpanzees and baboons. Fairgrieve (1995) and Sheppard (ongoing) have investigated in more detail the ranging and diet of *C. mitis* and *C. ascanius* in two compartments of logged and unlogged (Cynometra) forest. Both species have smaller range areas and greater potential food availability in the mixed (logged) forest. The effect of logging on the chimpanzee population is more difficult to assess as there is not one community with

a home range entirely within the unlogged compartment. Plumptre (1996) concluded that the geographical position within the forest block had a greater effect on the vegetation composition than the intensity of habitat disturbance. Rather than affecting species composition throughout the forest in any predictable manner. logging has affected the structure of the forest. Various measurements to assess forest structure showed that even fifty years following logging, forest compartments had not recovered to the level of structure of un-logged forests. Plumptre, Reynolds and Beresford-Stooke are now censusing primates densities in forest compartments immediately before and following logging in order to look at the initial behavioural response of the different species of primates.

2.6 History of Research at Budongo Forest.

Studies of the chimpanzees of Budongo Forest were initiated in 1962 by Reynolds and Reynolds (1965) and subsequently by Sugiyama (1968; 1969) and Suzuki (1971) All these field studies have had a similar orientation towards the ecology and social organisation of chimpanzees. In 1990 Reynolds returned to Budongo forest and later that year studies of the chimpanzees were resumed by Mr C. Bakuneeta with funding from The Jane Goodall Institute, National Geographic Society and USAID (Reynolds, 1992). In June 1991 The Budongo Forest Project was initiated with an orientation to the effects of logging on wildlife funded by the British Overseas Development Administration (Plumptre & Reynolds 1994; Plumptre et al. 1994; Plumptre et al. 1997). Work continues now with funding from the Norwegian Government Agency, NORAD. This project site is in a different location to the earlier work of Reynolds & Reynolds (1965).

2.7 Review of Previous Chimpanzee Research at Budongo.

Reynolds and Reynolds (1965) attained a total of 300 hours of direct observation of chimpanzees between February and October 1962 (170 days). Their study was concentrated in an area of approximately 16 square miles of forest on the north, east and south sides of Busingiro hill. The area consisted mainly of colonising forest (both Maesopsis and woodland) and mixed forest with some swamp forest but very

little ironwood forest (classified according to Eggeling, 1947). They concluded that the chimpanzees were primarily frugivorous, supplementing their diet with leaves, bark and pith and on rare occasions insects. The chimpanzees were observed to eat the fruit of 27 different species (90% of estimated total food bulk); the leaves of 9 species (5%); the bark and stem of 4 species (4%) and an unknown number of species of insects (1%). Later studies by Sugiyama (1968) between September 1966 and March 1967 also concluded that the chimpanzees in Budongo Forest were predominantly frugivorous in nature and that figs were the most important food. Sugiyama (1968) also observed that the seeds of Cynometra, (omitted from Reynolds and Reynolds (1965) food list, probably because of the time of year of their study) were important foods during the dry season December to March, at which time there were few figs in the forest. Sugiyama (1968) compared the seeds of *Cynometra* to that of *Brachystegia* in Tanzania, which had been observed in studies of chimpanzees at the Mahale research site to be an important food resource during the dry season.

At the time of the research by Reynolds and Reynolds the general social organisation of the chimpanzee remained ambiguous. Early observations usually reported encountering chimpanzees in small groups, and the family group (as had been documented in several monkey species) was commonly cited as being the social organisation of chimpanzees. Reynolds and Reynolds (1965) observed that the chimpanzees did not exhibit closed social groups. They observed that these groups were constantly changing membership, splitting apart, meeting others, and joining them, congregating or dispersing. They suggested possible factors which brought these groups together, namely the concentration of food supply, the presence of oestrous females, habit and friendship. Within these constantly changing groups or 'bands' 4 frequently seen types were distinguished 1) adult bands containing adults of both sexes, and occasionally adolescents, but not including mothers with independent young. 2) male bands containing only adult males. 3) mother bands, containing only with young and occasionally other females. 4) mixed bands, containing mothers with young, other females, adolescents and adult males. They also suggested that there was seasonal variation in the size of the groups. Chimpanzee movement and distribution through the study was observed to be

markedly affected by the ripening of fruit trees at different times and in different places. Larger groups of around 15 were usual when fruit was abundant interspersed with groups of 3 or 4 in periods between. Sugiyama (1968) also noted that the grouping patterns of chimpanzees were flexible and stated that "the troop may be dispersed into non-competitive foraging bands, of fluctuating membership, joining up at time of food abundance". He also suggested that chimpanzees in a forest habitat had a richer food supply compared to savanna woodland. This was based on the estimated lower population density at Gombe compared to Budongo (Sugiyama,1968). Reynolds (1965) described 'carnivals', prolonged periods of loud calls (pant hooting), perhaps when unaccustomed bands meet at food resources. A correlation between the size of groups and the amount and frequency of the outbursts was observed. Reynolds suggested that these calls and drums have the function of maintaining contact between groups, and communicating the whereabouts of food supplies.

Reynolds (1963) reported the use of habitual ranges instead of territories. No evidence of hostility between groups was observed, even when food was difficult to find. Animals in a region, although often dispersed in small groups were described as being bound together from infancy by ties of familiarity with a particular stretch of forest (Reynolds, 1963). Sugiyama (1968) also identified a regional population, distinct from the party, in which all individuals were connected by loose social bonds. This regional population was estimated to occupy an area of 7.5 sq. km. Forty one individuals were recognised and the whole population was estimated to number at least fifty six individuals. Again, Sugiyama did not observe any hostile interactions between regional populations. However, when Sugiyama (1969) played a tape recording of other chimpanzees pant hooting, a party of three chimpanzees suddenly stopped feeding, nervously searched under trees, but, finding nothing, climbed into the trees and scattered, each in a different direction. Perhaps, in the light of subsequent observations at this and other sites, this observation may be interpreted that antagonistic relationships did exist between regional communities. Both Reynolds and Reynolds (1965) and Sugiyama (1968) suggested that chimpanzees at

Budongo Forest do not suffer from a risk of predation and are therefore able to move alone in the forest.

Sugiyama (1968) was able to habituate the chimpanzees and recognise different individuals. He observed that males exhibited a strong social bond towards each other. They frequently moved in all male parties, and greater social interaction was observed between them, but was rarely seen between females. This is in contrast to observations of grooming bouts recorded by Reynolds and Reynolds (1965) which showed a very similar number records of grooming between both males and females. During his study, Sugiyama (1969) observed only 31 agonistic interactions. All incidences were between adult or adolescent males and no incidences between females were observed. Neither Reynolds and Reynolds (1965) nor Sugiyama (1968) found evidence for the existence of a dominance hierarchy with in the community.

A seasonal peak in copulation was clearly seen in December and January during Sugiyama's study (1969), when there was little rain, many trees shed their leaves and had little fruit. This is comparable to observations from Gombe, Goodall (1965). In Gombe, all observed instances of copulation's, except 3, occurred between early August and late November, during the dry season and ending just before the advent of the rainy season, however females with swellings were observed at all times of the year. Recent analyses by Wallis and Reynolds (1999) found there to be an important seasonal influence on the socio-sexual behaviour of chimpanzees at Budongo and Gombe.

Sugiyama (1969) suggests that hunting and meat eating of the Budongo chimpanzees must be much lower when compared with cases observed in the savanna-woodland of western Tanzania, where many cases of hunting and meat eating were recorded. Suzuki (1971) documented hunting of black and white colobus and was the first person to record and photograph 'cannibalism' or infant eating by chimpanzees. Observations from the present project have also confirm the occurrence of infant eating and cannibalism (Newton-Fisher, 1999a). Chimpanzees have also been observed to feed on black and white colobus, blue monkeys and duikers, although a successful *hunt* has yet to be observed. It should also be mentioned that individual chimpanzees are also chased by black and white colobus.

None of the earlier studies at Budongo documented the use of tools, even though during Sugiyama's study termite fishing had been observed in Gombe (Goodall 1965). The recent studies at Budongo Forest Project have established that tool use does occur in other contexts (Whiten et al. 1999). The chimpanzees are frequently observed to use leaf sponges to obtain water; leaf clipping, branch shaking are often incorporated into males copulation displays; leaves are used as 'serviettes' e.g. to wipe mouths after feeding on *Mildbraediodendon excelsum* and by females to wipe away semen following copulation. Chimpanzees have also been observed to use leaves as 'a background' on which to identify ecto-parasites (Asssersohn, in prep.). In addition, leaf grooming is also seen as an invitation to groom and branches are incorporated into the agonistic displays of the male chimpanzees. During this study the chimpanzees were also observed to feed on termites and honey without using tools. Other interesting food processing techniques included feeding on *Balsomocitrus dawei* by banging open the fruits on the trunk of trees; the extraction of rotting pith of *Rafia farinifera* by means of a relatively small opening in the side of the decaying tree; the swallowing of whole leaves of *Commelina sp.* for the mechanical removal of worms (Huffman et al., 1996).

Prior to this study, there have been two long-term studies of the behaviour and social organisation of the Sonso chimpanzee community (Newton-Fisher, 1997; Bakuneeta, in prep.).

2.8 The Sonso Chimpanzee Community

The chimpanzees of the Budongo Forest are of the eastern sub-species, *Pan troglodytes schweinfurthii*. During this study, the Sonso community included a total of fifty six identified individuals (see Table 2.5 and 2.7). The chimpanzees were classed into several different life history categories (Table 2.6). For the purpose of this study, which concentrated on the behaviour of independent individuals, all infants were lumped into one category, *infant*, and likewise all juveniles were lumped into one category, *juvenile*. In addition, *old* males and females were classified together as *adult*.

Table 2.5 Summary Of Age Classes Of Chimpanzees In The Sonso Community

Age class	Male	Female	Total
Adult	13	12	25
Adolescent	4	6	10
Juvenile	5	5	10
Infant	4	7	11
All	26	30	56

During the course of this study three adult males disappeared from the community; Chris, Kikunku, Zesta (Fawcett & Muhumuza, 2000), 1 adolescent female, Clea, and 1 juvenile female, Emma, emigrated into the community. Six infants were born into the community, Zig; unnamed infant of Kigere (stillborn), Rose, Rechel, Keti and Katia.

Table 2.6 Demographic Transitions Of The Sonso Community.

Age Category	Description
Infant 1	moving with mother, not yet weaned from mother's milk.
Infant 2	moving away from mother, feeding on foods other than mother's milk but not yet fully weaned. Still carried by mother
	Infancy terminated by birth of the next sibling
Juvenile 1	still close association between the mother and offspring, however the juvenile is now feeding and moving, on the ground and between trees, independently.
Juvenile 2	increasing independence from the mother. May or may not always be in the same sub-group as the mother. In the case of males, sometimes closer association with adult males. When feeding in the same sub-group they are often far apart from mother.
Adolescent male	development of testes. Beginning to challenge females for dominance
Adolescent female	beginning of sexual swellings, may be irregular. Initially, males are not very interested in female even when showing sexual swelling. As the female matures and shows full sexual swellings, she becomes more attractive to the males. No offspring.
Adult Male	testicular development complete. Face fully black in contrast to the pink face of younger individuals. Now dominates all females and challenges other males for position in hierarchy.
Adult female	now has own offspring.
Old male / female	baldness developing around the head and lower back. Much greying of hair.

Table 2.7 List Of Individuals In The Sonso Community During This Study. (DATE refers to the date first identified as a community member)

a) Adult Females (* = old)

NAME	CODE	DATE	OFFSPRING
BANURA*	BN	1993	BT, SH, ZF
HARRIET	HT	1996	HW
KALEMA	KL	1992	BH
KIGERE	KG	1992	KD, KE, still born 11/9/97
KUTU	KU	1992	KT, ?INF
KWERA	KW	1992	KZ
MAMA*	MM	1995	MH
NAMBI	NB	1994	NR, MS, AY, ?MU
RUDA	RD	1992	RE, BO
RUHARA*	RH	1993	RS, GT, NK
ZANA	ZA	1992	ZL, BB
ZIMBA	ZM	1993	ZG, GZ, KY

b) Adolescent Females

NAME	CODE	DATE	NOTES
CLEA	CL	1997	immigrant
JANIE	JN	1995	suspected immigrant
KEWAYA	KY	1992	mother Zimba
MUKWANO	MK	1992	suspected immigrant
SARA	SR	1995	suspected immigrant
VITA	VT	1993	occasional visitor

c) Juvenile Females

NAME	CODE	DATE	NOTES
EMMA	EM	1997	independent, no mother
GONZA	GZ	1993	mother ZM
GRINTA	GT	1993	mother RH
MUHARA	MH	1995	mother MM
SHIDA	SH	1993	mother BN

d) Infant Females

NAME	CODE	DATE	NOTES
BAHATI	BH	1994	mother KL
BETTY	BT	1996	mother BN
KATIA	KA	1998	mother KU
KETI	KE	1998	mother KG
NORA	NR	1996	mother NB
RECHEL	RC	1997	mother RD
ROSE	RO	1997	mother RH

e) Adult Males (* = old)

NAME	CODE	DATE	NOTES
Black	BK	1993	gamma male
Bwoya	BY	1992	
Chris	CH	1994	last seen Sept 97
Duane	DN	1993	alpha male
Jambo	JM	1993	
Kikunku	KK	1992	last seen June 98
Maani	MA	1992	
Magosi*	MG	1992	ex-alpha
Muga	MU	1992	?mother Nambi
Nkojo	NJ	1992	
Tinka	TK	1992	
Vernon	VN	1994	beta male
Zesta	ZT	1993	died 4/11/98

f) Adolescent males.

NAME	CODE	DATE	NOTES
Andy	AY	1994	mother Nambi
Nick	NK	1995	mother Ruhara
Bwoba	BB	1992	mother Zana
Zefa	ZF	1993	mother Banura

g) Juvenile males.

NAME	CODE	DATE	NOTES
Bob	BB	1992	mother Ruda
Gashom	GS	1994	independent, no mother
Kadogo	KD	1992	mother Kigere
Kato	KT	1993	mother Kutu
Musa	MS	1994	mother Nambi

h) Infant males.

NAME	CODE	DATE	NOTES
Hawa	HW	1995	mother Harriet
Kwezi	KZ	1996	mother Kwera
Zalu	ZL	1996	mother Zana
Zig	ZG	1997	mother Zimba

The kin relationships are based on observed association patterns or births. DNA analysis is not yet available for this study community. Immigrant and resident females are classified according to observations during Newton-Fisher (1997) study and this study. The only confirmed resident female, becoming an adult since this study, is Kewaya, she gave birth to an infant in 1999.

Vita is assumed to be in the process of emigrating in to the community. She is not seen on a regular basis and although she does have swellings, a full sexual swelling has not yet been observed. She appears to visit the community for a period of a few days only, during this time no hostile interactions with other community members were observed. In addition, Vita has not been observed to copulate with any of the community males. Clea was observed to immigrate into this community during this study. The immigration process was relatively quick. Initially, she was observed to visit the community only when in full oestrus, during these periods she would only associated with large mixed groups or otherwise all-male groups of chimpanzees. She remained on the peripheral of the group, and was not of any particular interest to the male chimpanzees. Over the course of 1998, she gradually changed her patterns of association to ranging with the alpha female, Nambi. On one occasion she was seen playing with Nambi's infant Nora. There were many agonisitic interactions between her and the other adolescent females.

Sex Ratio

The sex ratio of sexually mature males to females was particularly unusual during this study. At other study sites the chimpanzees are found to have a sex ratio in favour of females. At Tai, this is interpreted as a result of higher mortality rates of adolescent and adult males, (Boesch & Boesch-Achermann, 2000). At the beginning of this study the number of males was greater than that of females and during the course of the study three adult males disappeared, 2 without known cause, and the third the suspected result of intra-community aggression (Fawcett & Muhumuza, 2000).

2.9 Other Chimpanzee Communities.

There were a few sightings of other of groups of unhabituated chimpanzees. These sightings were confined to the Nature reserve (forest compartment N15) and to the south west of the *Royal Mile*, a section of road leading to camp (forest compartment N1). A male with a missing right foot was observed to be present in both these areas. Therefore, it is suspected that it is the same community. Another community

boundary was suspected to lie to the north of the grid system. Patrolling behaviour of chimpanzees was seen in this area.. Compared to the ranging behaviour described during Newton-Fisher's study (1997), the area to the east of the grid system referred to as Kasenene Hill (Waibira) was used very rarely during this study. Occasionally, distant calls could be heard which were not responded to by the study community. It therefore seems likely that a territory boundary existed there. During this study the area SE of the grid system and south of the Royal Mile and into the village of Nyakafunjo were used for the first time. It is unlikely that the boundary areas are well delineated as both at the nature reserve and along the *Royal mile* unknown chimps were observed within areas where the Sonso community was also observed. Only one direct community encounter was witnessed. This event occurred within the eastern boundary of the nature reserve. The Sonso community were feeding in *Cynometra*, they replied to some nearby calls, (we initially assumed that these were from another party of Sonso chimpanzees), by rapidly climbing down and moving towards the east. The Sonso community were relocated about 200m east, again feeding on *Cynometra*. As Geresomu and I stood beneath the tree trying to identify all individuals, two unknown males charged through the undergrowth, directly past us. The response of the only male on the ground, KK, was to turn and run east. Upon seeing us the unknown chimpanzees ran back immediately. The attack occurred near a river. The outcome of the encounter was ambiguous. According to the sound of pant hoots and observations of the Sonso community, the Sonso males continued to move slowly north east of the river and the other community moved towards the south. It is probable that the presence of human observers affected the outcome of the attack as when we were spotted by the charging males, they stopped and ran back to the south, where other community members were spread out in the trees.

Chapter 3

General Methodology

3.1 General Overview

The aim of this chapter is to give an overview of the methodologies used to collect data during this study. In particular, much of the behavioural data was collected simultaneously using the same check sheet and then later separated for analyses.

Field data were collected continuously between January 1997 and December 1998, a total of 24 months. The data were collected by myself and two field assistants Geresomu Muhumuza and Julius Kyamanya. After the establishment of the phenology trail Julius was responsible for the collection of the phenology data. Julius had previously collected phenology data for the Budongo Forest Project and was therefore highly skilled. Geresomu had previously worked with the Sonso community of chimpanzees with Nick Newton-Fisher on his study of male chimpanzee social behaviour, (Newton-Fisher, 1997) and also on various vegetation orientated projects with other students and for the Budongo Forest Project. Geresomu's knowledge of the chimpanzees and the forest was critical to this study. He patiently taught me the identification of the individuals in our chimpanzee community and the plant species they were feeding on. Geresomu and I worked together to collect the behavioural data and were able to ensure the continued collection of data during periods when one or another of us were absent from the field. I was in the field in two sessions; January -June 1997 and then September 1997 - December 1998. Most of the data analysed in this study are from the period June 1997 to December 1998. The period before this was used as a pilot study for learning individual recognition of the chimpanzees and establishing the methodology protocol. Phenological data is available from September 1997 - December 1998. During the main study (June 1997- December 1998) 1324 hours of systematic behavioural data were collected.

3.2 Temperature and Rainfall.

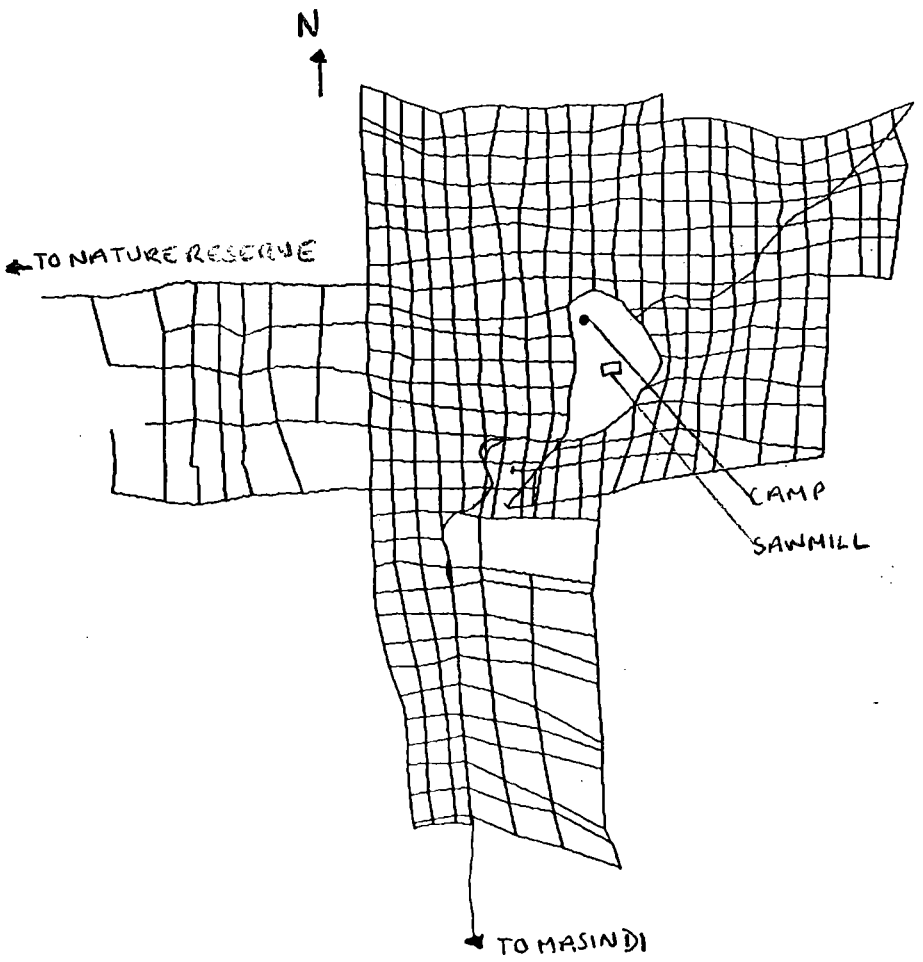
Temperature and rainfall data were collected by the staff of Budongo Forest Project. Rainfall data were collected using a rain gauge in an open area approximately 10m from the forest edge. Temperature data were recorded as the mean between two readings taken in the shade at the edge of the forest. The readings were taken at approximately 0700hrs each morning.

3.3 The Trail System.

There is a cut system of trails through the main study area of the forest (Fig 3.1). The width of each trail is approximately 0.5m. The trails are cut 100m apart forming 100m x 100m forest blocks which were used to provide location data.

In many areas of the forest, the use of trails was essential to following travelling groups of chimpanzees. The chimpanzees also would often use the trails to move through the forest. During this study the trail system was extended to the south to aid the following of chimpanzees and to obtain more accurate patterns of range use. The trails were cut and mapped using a compass and both pacing and a tape measure to measure distance.

Fig 3.1 Map Of The Trail System In The Study Area



3.4 Phenology Data Collection

In order to assess the availability of food in the study area the phenology of twenty six tree species, (a total of 378 trees), known to be eaten by chimpanzees from previous studies in Budongo and other sites was monitored every two weeks. The percentage canopy cover (phenology score) on a scale of 0-4 (including 0.5 intervals) of mature leaves, young leaves, leaf buds, ripe fruit, unripe fruit and flowers were scored for each tree canopy. In addition, all records of fruiting trees were noted as the trail was walked. The density of chimpanzee food tree species was assessed by 24 transects 200m x 10m. A total of 825 food trees were sampled along these transects

3.5 Chimpanzee Behavioural Data Collection

Pilot study

The period between January 1997 and June 1997 was used as a pilot study to consolidate data collection techniques. This was quite an extended time period due to extreme difficulties at the onset of the project in locating chimpanzees. The exact reason why the chimpanzees were so difficult to find is still uncertain. At this time there were four experienced chimpanzee field assistants and myself searching for chimpanzees with little success. The chimpanzees appeared to be moving over large distances and were seen in areas, seldom used before, out-with the trail system. When we did locate the chimpanzees, often having seen us, they would then flee from the tree, as if unhabituated. January is usually a period of drought and assumed low food availability. During times of low food availability chimpanzees are predicted to forage in small parties and to give fewer food calls thus making it more difficult for the observer to locate parties. At the beginning of 1997 there was a particularly harsh drought, with no rainfall being recorded for two months (see Chapter 2). The depleted food resource base within their own community home range may have resulted in the chimpanzees ranging more widely in search of food and having to search within neighbouring communities home ranges, this in turn may explain their nervous behaviour. Another thought was that the presence of pit-sawyers in the area may have disrupted the chimpanzees from ranging within their

usual home range. However, this did not seem to be a problem later in the study. After three months the chimpanzees returned to ranging in their frequently used area .

3.6 Habituation and Visibility Levels

There have been on-going studies of the Sonso chimpanzee population since 1991. Habituation of the chimpanzees was initiated by Chris Bakuneeta and a team of field assistants. Further study by Newton-Fisher (1997) intensified the habituation of the male chimpanzees. During this study, after the chimpanzees returned to ranging within the usual home range area, the habituation problems (i.e. chimpanzees fleeing from trees) vanished. The present study was the first study to concentrate on the behaviour of female chimpanzees. Observations from other study sites have found that females take longer to habituate than males (Goodall, 1986; Boesch & Boesch-Achermann, 2000). This is probably due to a combination of offspring protection, the generally more solitary nature of female chimpanzees compared to males, and an observer bias towards following the often larger and noisier groups of males. Newton-Fisher (1997) also noted that the lowest ranking males took the longest time to habituate. Newton-Fisher (1997) states that he accelerated the habituation process by "continually pushing the limits of the chimpanzee's tolerance". This is not a technique that I employed to continue the habituation of the female chimpanzees. I preferred to remain quietly with the chimpanzees and allow them to develop trust and confidence in our presence. Individual identification of less social animals is also difficult unless there is an obvious facial feature, e.g. slit in ear. Therefore some time was spent during the pilot study identifying all the females present in the community. By the beginning of the main study we were both confident in the identification of all members of the community. Habituation levels of the females had also improved. However, although some individuals would allow us to observe them on the ground, the majority of individuals would not. As a result the majority of observations in this study were limited to times when the chimpanzees were present at feeding trees. Generally, the success rate of following larger parties was greater than smaller or lone individuals. Even when following larger sub-groups of chimpanzees the alpha male, Duane, would often sit between the observer and the other chimpanzees as they

passed by, acting as a 'protector'. Similar behaviour was also noted by Reynolds (1963).

During the course of this study, as the habituation levels of the chimpanzees were improving, it was decided by all working at Budongo Forest Project to introduce a 5m rule. This meant that no observer should ever be any closer to chimpanzees than 5m. We were all of the view that the observer should interfere as little as possible in the activities of the chimpanzees. The 5m rule should also reduce the possibility of cross species disease transmission in either direction[1].

Visibility levels in the forest were generally quite poor. "Inside the forest it was impossible to distinguish chimpanzees on the ground as they were merely black shadows in the undergrowth" Reynolds & Reynolds (1965). Things have not changed! Especially in areas where extensive logging had taken place visibility on the forest floor was limited by the dense vegetation, often climber tangles. No quantitative measure of visibility was taken but usual, although still obstructed by vegetation, views were 10m or less when on the ground. It was difficult to follow chimpanzees on the ground without using the trail system. The dense lower levels of vegetation made it difficult for the observer to move quietly behind a small party of chimpanzees at a distance which was close enough to maintain visual contact but at the same time far enough away to not frighten the chimpanzees.

3.7 Location of chimpanzees

Chimpanzees were located using one or a combination of four techniques.

- visiting known fruiting trees and in some instances waiting for the chimpanzees to arrive.
- following the direction of chimpanzee vocalisations

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[1] **Note**: The decision to habituate a community of chimpanzees is a difficult one. During this project the occurrence of crop raiding by this community increased compared to previous years. This might be as a consequence of the patterns of food availability within the forest, but it may also be because the chimpanzees are no longer afraid of humans. Should the project now accept responsibility for the farmers lost crops? On the other hand, the chimpanzees, their fear of humans now removed, are now at a greater risk of being poached and hunted.

- chance location of individuals in the forest.
- returning to the area where the chimpanzees had nested the night before.

The methods used would vary according to the behaviour of the chimpanzees. In practice all of these methods would commonly be used within one morning. For example, we would set off in the direction where the chimpanzees were sighted the previous day, heading for known fruiting trees in that area; however if calls were heard we would then head in the direction of the calls as they were the most consistently reliable method of locating chimpanzees, and calls also presented the opportunity to find chimpanzees in other areas of the forest, identify new fruiting trees, resulting in a complete picture of their ranging patterns. Once a party of chimpanzees was located, the decision to stay with them or to look for another party was dictated by the presence of particular individuals within the feeding party and the perceived likelihood of finding another party of chimpanzees. Occasionally, we would come across chimpanzees in the forest by chance. However, as a rule randomly searching the forest for chimpanzees was not productive. When we had absolutely no idea of the whereabouts of the chimpanzees we would visit particular sites in the forest which offered good auditory conditions, i.e. slightly elevated or a small clearing, and sit and wait for calls. Listening for calls whilst walking was not productive. As the focus of this particular study was the behavioural ecology of female chimpanzees extra efforts were made to search all possible locations for chimpanzees. Female chimpanzees are known to be less vocal and the study was attempting to record the ranging patterns and feeding behaviour of females associating not only in the usually larger and noisier male groups but also alone or in all-female nursery groups. Over the course of a day we would attempt to visit all known fruiting trees and were constantly monitoring trees which we were expecting to come in to fruit. Particular attention was targeted at the periphery of the male community range, as established by Newton-Fisher (1997), as these areas were believed to be the most important for addressing the community membership concept in chimpanzee social organisation. We would also ask other researchers which individuals/trees they had encountered and attempt to also locate these chimpanzees.

3.8 Chimpanzee Behavioural Sampling

Two levels of decision need to be made when deciding on systematic rules for the recording of behavioural data (Martin and Bateson, 1986). The first, *sampling rules*, specifies which subject to watch and when. This covers the distinction between ad libitum sampling, focal sampling, scan sampling and behavioural sampling. And the second, *recording rules*, specifies how the behaviour is recorded. This covers the distinction between continuous recording and time sampling. During this study, data were collected using a combination of focal sampling, scan sampling and ad libitum sampling rules and both continuous and time sampling recording rules.

Overview

All behavioural data were collected using a combination of checksheet (see Appendix A) and notebook and pencil. We both used binoculars (magnification 7 x 40 Geresomu; 10 x 42 Katie) and TIMEX (ironman) watches to record the time. A compass and pacing by foot were used to record locations off the grid system. During the course of this study there were three other students and four other field assistants together in the field all conducting different chimpanzee studies and with differing priorities for individuals to be selected as focal animals. For this reason we attempted to use VHF radios to maintain contact with other researchers in the forest. However, this was not a huge success. Due to the flat nature of Budongo Forest it was difficult to get the base station high enough to receive signals from a wide area. Also there was a problem assigning someone to operate the base station. In addition, individual to individual radio range was very short (approx. 400m) and there were further problems with solar power supplies to recharge the radio batteries. Therefore, the use of radios was stopped. However, we continued to swap location information at lunch times and evenings.

On initial contact with a party of chimpanzees all individuals were identified by myself and Geresomu. Once identified, the arrival or departure of individuals to and from the party were recorded continuously. Geresomu and I worked together in order to monitor the group activities. It was often not possible for one observer to have the whole party of chimpanzees in their field of view. When attempting to

follow individuals on the ground one observer would follow behind the chimpanzees as they moved through the forest, the other observer would move along the trails spotting the chimpanzees as they crossed/joined trails. In addition, Geresomu collected information regarding the party as a whole using the checksheet and I would collect focal animal data using the notebook. When working alone we would each only collect checksheet information.

Definitions Terminology

***Community*:**

The same as unit-group used by Japanese researchers (Nishida, 1979; Sugiyama & Koman, 1979). A collection of individuals associating together in a fluid, fission-fusion fashion, ranging over a common area. Relationships between different communities are usually hostile (Goodall, 1986).

***Party*:**

The same as sub-group (Nishida, 1968) or band (Reynolds, 1963). A behaviourally cohesive group of individuals. In practise this was within an approx. 35m radius. Party size was measured as all independent individuals within the observer's view (and thus assumed to be within possible view of each other). The observer would move around the edge of the party or beneath the feeding tree to search for all individuals.

***Independent individual*:**

any individual who has been weaned and which usually joins parties independent to the choice of its mother.

Feeding patch:

Preliminary observations suggested that the chimpanzees were highly selective in their choice of food species. The majority of observations of feeding parties were at single trees. Therefore a feeding patch was defined as an individual tree, (in a few instances it may be more than one if the tree has overlapping or adjacent crowns). The size of the feeding patch was assessed by the diameter at breast height, DBH, (or sum of) and the individual tree phenology score.

***Food item*:**

a food item is defined as the combination of species and the part of the plant being eaten. In the case of animal matter only the species was recorded. Plant parts recorded were Fruit: ripe/half-ripe/unripe; Leaves: young and mature; pith; bark; flowers and seeds.

***Oestrus State*:**

sexual swelling of all females was recorded on a scale of 0-4. For analysis purposes the following categories were used 0= no swelling or 'flat'. 1-2 some degree of swelling, 3-4 maximal swelling (stage at which the majority of copulations occurred).

Collection of Scan data

This was collected by Geresomu every 15mins and started once we had identified all individuals within the party. Scan sampling means that a whole group of subjects is rapidly scanned or censused at regular intervals and the behaviour of each individual at that instant is recorded. The behaviour of each individual scanned is, necessarily, recorded by instantaneous sampling (Martin & Bateson 1986). This technique enabled data to be collected that were evenly representative across all individuals, time of day and season. This is later used in behavioural and ecological comparisons between males and females and different age classes.

The following information was collected every 15 min:

Date:

Time:

Location: recorded using the co-ordinates of the 100*100m blocks of the trail system

***Party Composition*:** all independent individuals present.

Activity: the behaviour of all independent individuals; see Table 3.1

Distance: of independent individuals from focal animal up to a maximum of 25m (this was the distance judged to be estimated accurately).

***Oestrus State*:** oestrus state of all independent females; scored 0-4.

food item: the species and part and phenology state.

***food patch size*:** the diameter at breast height, (DBH), of the feeding tree and its phenology score.

If an individual was seen present on scan A but not the next (scan B), then present again on the subsequent scan (scan C), and was not seen to have left and rejoined the party, then the individual was recorded as being present for all three scans. The activity of an individual was only recorded if the observer succeeded in having a clear view of the focal subject.

Table 3.1 Behavioural Classifications:
The individuals involved were recorded for each event, and the direction of behaviour indicated with arrows. i.e. who approached, initiated the behaviour and the outcome of the behaviour. The notebook was used to describe social interactions in more detail.

Behaviour	Code	Description
Copulation	COP	all copulations; noted oestrus stage of female.
Foraging	FE	feeding: the direct ingestion of food items.
	FO	foraging: any activity involved in the direct gathering of food.
	FW	wadging: the chewing of many fibrous foods before ingestion.
Grooming	SG	any self directed grooming behaviour.
	GA	any grooming behaviour directed at another individual.
	GR	any grooming behaviour received from another individual.
	SC	any self directed scratching behaviour
Locomotion	MOG	travel on the ground, usually between feeding patches
	MOT	moving in trees, usually relocating within a feeding patch.
	CMU	climb up: usually entering a feeding patch/joining a party.
	CMD	climb down: usually leaving a feeding patch/leaving a party.
Nest Building	NC	construction of day or night nest.
Play	PL	play behaviour, usually involving infants.
Resting	RS	default category, when no other behaviour is apparent.
	RSG	resting on the ground.
	RSL	resting lying down.
	RSN	resting in a nest.
Social Behaviour	SOC	described in notebook.
Vigilant	VIG	intent gaze
Vocalisation	VOC	pant hoot, food grunts, pant grunt and screams

Any social data involving in particular female chimpanzees was described in more detail in the notebook. This included social behaviour recorded during scan and *ad lib.* social data collection. All dominance interactions between females were recorded

in this way, these included pant grunts, (a submissive vocalisation given to confirm dominance relationships), agonistic interactions, (physical aggression, chase, displace from feeding patch; and the insertion of a finger in the vagina of another female). An effort was made to record as detailed a record as possible, including the initiator and recipient of the behaviour, the context of the behaviour, feeding, resting, sexual, no apparent context, and the outcome of the event. Initially, during focal animal data collection an attempt was made to record all self directed scratching behaviour. This has been shown in other studies to be a good indicator of behavioural anxiety (Baker & Aureli, 1997). However, the practicalities of recording such behaviour in the field were immense. It was not usual to have a complete and unobstructed view of the chimpanzees, therefore many acts of scratching may be unnoticed. In addition, both visibility and perhaps the behaviour itself made interpretations of rough scratching and usual gentle scratching ambiguous.

Focal Animal Data Collection

Focal animal sampling means observing one individual for a specified amount of time and recording all of its behaviour. Ideally, the choice of focal animal is determined prior to the observation session. Focal sampling is generally the most satisfactory approach to studying groups (Martin and Bateson, 1986). In this study, focal animal sampling, using behavioural sampling (Martin and Bateson, 1986), was used to gather data on social behaviour. The prime reason for using focal animal sampling was that it concentrated the observer on the activity of one individual. This is important when recording behavioural events. Without using focal sampling the observer may for instance notice a copulation occurring but not have noticed by whom it was initiated. This is perhaps a particular problem in low visibility conditions and with chimpanzees which form groups over areas which are too great for the observer to simultaneously watch all individuals. Behavioural sampling allows the collection of data to concentrate on the behaviours of interest. In this study we were particularly interested in the social behaviour of female chimpanzees, which is usually thought to be less conspicuous and less frequent than that of males. Particular attention needed to be paid to the occurrence and direction of pant grunts

as these were relatively quiet vocalisations usually unaccompanied by another gesture. Although, bobbing of the body and repetitive pant grunting may occur during contest situations or when there is an extreme difference in rank between two individuals. This was usually only apparent between males and adolescent females.

Initially, it was intended to locate and then to follow individual independent female chimpanzees for as long as possible, ideally from nest to nest and to balance the number of hours of observation of each individual over each month. However, many difficulties were encountered with this method. The primary difficulty was in following individual chimpanzees when they moved away from a party or feeding patch. Due to a combination of visibility, habitat and habituation levels it was nearly impossible to follow chimpanzees on the ground. The situation was marginally better if there was more than one chimpanzee in the party as the chimpanzees would then be less shy and less averse to being followed. Large groups were the easiest to follow as party members would frequently call to each other as if to maintain contact as they travelled from one location to another. Another problem was that some of the shier adult female chimpanzees would not leave the feeding tree with the rest the of the party if there was a human observer below on the ground. This resulted in the situation where the observer would wait patiently beneath the tree, the chimpanzee would then nest for 1.5 to 2 hours and then would move away silently in the trees and be 'lost ' to the observer's view within minutes. Not only did this mean that the focal individual was lost but also the previous chimpanzee feeding party, source of an alternative focal individual, had also now moved on to unknown whereabouts. I also felt unsure if the individuals behaviour had been altered by my presence. The situation was amplified if there was a large group of observers under a feeding tree and the party decided to come down to the ground and move on, although it was possible to keep track of the main party, (and many observers facilitated this), it was not always possible to keep a particular focal individual in sight. This was particularly difficult with the shy female chimpanzees. Due to the number of researchers in the forest it was quite common for 6 or more people to be under one tree collecting different sets of data from a single party of chimpanzees. The number

of researchers and field assistants did have the advantage of being able to cover larger areas of forest when searching for chimpanzees.

As a result of the above methodological problems, in January 1998 it was decided to adjust the length of the focal sample to 30mins and to introduce a sampling rule that an individual should only be sampled once per day. This gave extra flexibility to move around the forest and the opportunity to encounter as many different parties as possible. Unfortunately, with this decision the opportunity to record day-range length was lost. That said, day range length data may only be considered accurate when collected from communities which are fully habituated to having observers follow them on the ground. During focal animal sampling the same behavioural categories were used as in scan sampling (Table 3.1). Focal samples were conducted on adolescent and adult females and males, in order to evenly sample community members. Previous to this, focal samples had only been conducted on adolescent and adult females. On contact with a group of chimpanzees the order of sampling was decided according to which individual had the least number of completed focal samples. As stated previously, the decision to stay with a particular party and choice of focal subjects was made based on the perceived likelihood of finding another party or community members. Scan data continued to be collected at 15min intervals and was expanded to include the activity patterns of all individuals in the party. The number of scans and the number days of each individual was observed per calendar month are shown in Tables 3.2 & 3.3.

Ad Lib Data Collection.

During *ad lib* data collection no systematic constraints are placed on what is recorded or when. The observer simply notes down whatever is visible and seems relevant at the time. This results in biases towards those behaviour patterns which are conspicuous, however it is useful for recording rare events (Martin and Bateson, 1986). It was used during this study to record all aspects of female social behaviour in particular dominance events, copulations and grooming. Both Geresomu and I collected *ad lib.* data when the opportunity arose.

Table 3.2 Number of Days per Month each Individual Sighted. (refer to Chap. 2 for identification codes).

	1997							1998												
	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Adult females																				
BN		1	1		18		1		1	8	4	2	1	1		1	5	4	1	49
HT			1		2	4	4	2		1	4					4	5	5	1	33
KG		4	10	7	9	11	8	9	2	10	9	7	1		6	4	12	2		111
KL	1	5	13	4	13	8	4	3		8	11	5	5	3	16	2	9	9	2	121
KU		6	2	3	8	9	5	3	6	14	10	3	8	4	7	8	13	5	2	116
KW	1	8	15	9	10	10	5	1	7	15	12	8	6	6	18	2	14	8		155
MM		5		1	3	1			1	3	1		1		3					19
NB	1	7	13	7	13	12	4	6	4	14	3	11	9	4	12	12	9	12	4	157
RD		6	3	1	2	4	3		3	57	51	18	3		4	1	3	4		163
RH		1			5	8			2	13	11	5	3				8	4	1	61
ZA		3	2	2	6	12	3		9	4	6	8		1	7	2	3	1	1	70
ZM	2	9	13	6	6	11	8	3	3	10	10	13	5	7	15	6	10	5		142
?FEM			1		2	3		1	4	12	1	3			3	1				31
Adolescent Females																				
CL			2	5	15	12	9	4	6	13	12	8	8	4	6	15	20	10	3	152
JN		4	6	5	14	9	8	11	8	16	11	14	7	4	10	14	19	11	5	176
KY		3	13	8	12	11	7	8	7	15	13	11	4	4	13	9	14	4		156
MK		7	14	7	11	9	1	6	7	13	8	9	1	2	7	1	15	10		128
SR		4	6		13	11	4	1	4	15	11	5		1	1		9	10	1	96
VT		3	2			2	3		1	3	2	2						1		19
?SAF			1						1											2
Juvenile Female																				
EM				3					2	7	5	6	3	2	3	6	17	9	1	64
Adult Males																				
BK		1	8	4	13	9	8	10	12	18	10	7	5	3	7	10	13	11	4	153
BY		4	8	3	11	7	2	5	8	16	8	9	5	2	2	6	8	10	4	118
CH		2	3	1																6
DN	1	4	13	7	15	8	2	8	10	16	13	9	2	5	9	14	16	11	5	168
JM		5	5	1	4	3	2	5	7	11	4	6	5	2	6	5	10	10	3	94
KK	1	3	10	12	15	14	4	9	10	19	15	12	9	1						134
MA	1	8	11	5	15	10	6	8	4	19	12	11	8	4	4	6	17	13	5	167
MG		2	14	2	6	9		9	9	20	13	12	9	6	13	10	18	10	1	163
MU		6	13	6	11	5	6	2	5	16	12	8	11	4	4	8	7	15	3	142
NJ		2	12	7	16	8	10	8	12	20	13	9	6	4	3	7	16	11	5	169
TK	1	6	8	1	2	2	1	3	1	9	9	5	8	5	8	8	9	12	2	100
VN	1	3	11	5	11	8	4	10	6	16	8	3	3	3	11	9	12	10	3	137
ZT		7	9	9	15	8	5	8	6	19	12	10	10	3	11	12	16	4		164
Adolescent Males																				
AY	1	7	13	7	14	7	6	10	8	18	5	12	12	5	14	11	16	10	5	181
BB		4	12	6	13	10	5	4	7	9	11	6	3	5	16	10	15	12	4	152
NK		1	4	4	12	7		7	9	15	11	6	3	1	7	9	11	13	4	124
ZF		6	7	2	11	7	2	1	2	6	8	12	5	4	11	10	14	8	4	120
Juvenile Male																				
GS		6	8	8	10	10	3	5	8	15	11	8	10	5	10	7	12	13	1	150

Table 3.3 Number of Scans per Individual per Month (refer to Chap. 2 for identification codes)

	1997								1998										
ID	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Adult Females																				
BN		4	11		4		6		9	89	29	8	6	3		9	28	33	9	248
HT			21		33	28	32	12		1	42					25	20	29	3	246
KG		47	119	83	90	81	52	57	7	38	71	59	4		30	31	80	15		864
KL	7	51	150	21	106	73	17	16		47	114	19	38	23	118	16	238	42	8	1104
KU		75	13	35	69	76	17	28	24	92	139	17	69	24	33	49	81	16	15	872
KW	4	90	127	55	84	96	39	4	29	130	108	38	27	30	132	7	111	31		1142
MM		88		1	24	10			3	18	14		12		19					189
NB	7	70	89	56	99	67	20	24	20	103	103	68	58	25	95	105	56	65	31	1161
RD		96	32	10	2	29	22		10	1	6	10	3	1	19	7	20	15		283
RH		16			66	69			15	83	88	36	15				63	29	6	486
ZA		34	22	8	76	109	32		30	36	63	61		3	67	20	13	8	6	588
ZM	44	127	81	35	73	125	52	20	16	62	88	100	21	38	150	30	70	27		1159
?Fem			1		13	35		8	30	58	6	38			20	1				210
Adolescent Females																				
CL			10	19	133	97	83	23	25	68	95	68	42	42	36	119	161	83	28	1132
JN		41	30	17	119	102	88	89	43	91	112	116	43	28	82	165	134	102	38	1440
KY		15	87	53	72	84	57	69	18	106	95	78	7	20	98	45	81	28		1013
MK		71	64	48	141	64	31	46	31	80	75	75	2	4	35	3	106	46		922
SR		35	31		86	137	39	4	13	115	79	41		3	3		56	63	9	714
VT		26	8			26	10		3	11	5	37						11		137
?SAF			1						4											5
Juvenile Female																				
EM				23					13	50	17	1	24	4	35	34	67	46	3	317
Adult Males																				
BK		5	35	17	107	38	67	44	46	82	137	38	17	18	74	97	77	93	31	1023
BY		21	43	7	25	56	9	35	66	94	109	48	6	2	19	57	42	101	36	776
CH		5	7	3																15
DN	6	14	68	17	89	84	9	59	57	111	133	74	4	49	73	137	101	103	48	1236
JM		47	14	1	23	13	17	25	46	36	35	61	23	8	50	38	53	71	19	580
KK	2	20	42	30	130	72	39	54	77	142	132	117	46	3						906
MA	3	66	49	22	101	43	73	42	31	104	131	9	45	38	29	39	120	122	40	1107
MG		13	69	9	12	44		45	48	122	128	95	69	31	96	64	89	62	3	999
MU		54	67	15	75	23	48	11	15	96	106	52	64	27	45	60	25	78	20	881
NJ		9	37	16	135	31	99	44	67	115	107	57	46	19	9	75	92	72	27	1057
TK	9	65	40	1	13	2	9	18	10	58	97	23	34	6	42	70	56	89	18	660
VN	6	25	65	16	58	40	16	55	31	94	61	16	14	39	80	62	68	108	25	879
ZT		57	52	21	126	32	46	52	43	140	115	61	48	9	61	96	102	26		1087
Adolescent Males																				
AY	4	59	78	25	96	71	42	52	23	126	160	77	66	23	132	90	109	109	39	1381
BB		29	91	31	97	28	55	32	27	65	109	36	25	10	101	58	93	89	34	1010
NK		16	21	17	104	24		53	29	126	130	58	18	1	63	87	85	107	25	964
ZF		36	19	7	57	56	3	5	9	31	42	64	29	14	56	84	70	50	32	664
Juvenile Male																				
GS		60	78	16	54	42	20	27	36	96	78	42	74	11	55	40	84	102	8	923

3.9 Faecal Data Collection

A total of 161 faecal samples were collected in order to provide additional information on chimpanzee feeding behaviour. All complete and fresh faecal samples were collected whilst following the chimpanzees. Only complete samples were collected in order to compile a complete record of the proportion of food items in the chimpanzee diet. Dung samples were collected between January and December 1998. Plastic bags were used to collect the samples and labelled using a permanent marker pen, recording the date, time and location collected. Only faecal samples located well within the home range area were collected or those which we knew were directly from our community. It was thought important to collect fresh samples before dung beetles etc. had a chance to remove parts of the samples, in addition to plant material decay. The samples were then washed in the Sonso stream and passed through a 1 mm sieve. After washing the contents, scores were assigned to each sample according to the abundance of each component in the sample. Scores for the abundance of each category in the sample were given on a scale of 0-4 including ½ scores. Categories used were seeds (large seeds were also counted), Fruit flesh/skin, leaves, Pith and other (includes soil, bark, insect). A list of all food items, identified to species level where possible was recorded. Fruit seeds were usually identified to species level, however with some species identification was only possible to genus (i.e. *Ficus* sp.).

Chapter 4

Patterns of Food Availability

4.1 Introduction

Phenology Patterns

Traditionally, the productivity pattern of tropical forests has been regarded as being non-seasonal, in contrast to the distinctly seasonal character of temperate forests. However, although the overall appearance of the tropical forest may vary little during the year, the activities and rhythms of species within the forest are constantly changing and are subject to a wide diversity of selective pressures. It is these changes in the availability of leaves, flowers and fruit of the various food species which are important to the animals living within the forest. Some plant foods may be available throughout the year, others may fruit reliably at the same time each year and others may have reproduction patterns which appear random. However, detailed studies have shown that in general, the tropical forest community as a whole has periods of fruit, flower, young leaf and bud abundance, and corresponding periods of food scarcity. These periods of abundance and scarcity have been linked to changes in climatic variables e.g. rainfall, temperature, hours of sunlight, day length (Tutin & Fernandez, 1993a; van Schaik et al., 1993; Wright & van Schaik, 1994; Newbery et al., 1998; Tutin & White, 1998; Chapman et al., 1999). Changes in food abundance may occur not only on an annual basis, but many long-term studies have also reported variation in the inter-annual availability of food (Tutin & White, 1998; Chapman et al., 1999) and even between different sites in the same forest (Chapman et al., 1997, 1999). As the availability of food items is in constant flux, so also are the diets of the primary consumers. Leighton & Leighton (1983) found that the preferred foods of frugivorous birds and mammals vary greatly in abundance from month to month and also inter-annually. There are two strategies available to foraging species when the preferred food item is temporarily unavailable;

- extend ranging patterns in order to maintain a similar level of selectivity. The hornbill being the extreme example which migrates (Leighton & Leighton, 1983).
- maintain usual range areas and shift diet to other available foods. These may be of lower quality and therefore lead to an increase in the time spent feeding or alternatively an increase in time spent resting in order to reduce energy expenditure (Terborgh, 1983).

This study will assess the extent of fluctuations in food supply experienced by the Sonso chimpanzee community during the study period and document the dietary and behavioural responses of the chimpanzees.

Keystone Resources

Studies of the fluctuation in food availability are also important in order to identify keystone or fallback plant species for the animal communities of a tropical forest. Keystone resources, must by definition, be available to the consumer consistently either year round (as in the case of mature leaves, bark and fruits and seeds of common species which reproduce asynchronously) or during regular, seasonal periods of succulent fruit scarcity (Tutin & White, 1998). Previous studies by Sugiyama (1968) identified *Cynometra alexandrii* seeds as being a possible crucial resource during the January dry season for Budongo chimpanzees.

Relevance to socio-ecology

Knowledge of the relative abundance and spatio-temporal distributions of food resources may also contribute to the understanding of the influence of ecology on chimpanzee social organisation. Recent studies have concentrated on assessing differences in ecological resource bases and possible associated differences in social organisation and structure between different communities of both *Pan troglodytes* and *Pan paniscus* (White & Wrangham, 1988; Chapman et al., 1994; Malenky & Wrangham, 1994; Malenky et al., 1994; Wrangham et al., 1996). As yet, however, few studies of habituated chimpanzees include detailed phenological data, the exceptions being Kibale Forest, Uganda and Lomako Forest, Democratic Republic of Congo. Variation in food supply has also been hypothesised to be a selective pressure

for tool use. Tool use to access food, increases during periods of food scarcity in the Bossou community of chimpanzees (Yamakoshi, 1998).

4.2 Aims

- to identify patterns in the availability of different plant foods.
- to identify climatic factors which may influence changes in food availability.
- to assess the validity of different methodologies to assess food abundance.
- to compare the availability of chimpanzee food species to that of the whole forest community
- to identify possible fallback or keystone resources for the Sonso community of chimpanzees.

4.3 Methodology

Methods used for assessing food availability can be divided into three broad categories:

- use of fruit traps to count/weigh all fallen fruit.
- a systematic transect system, monitoring all trees within the transect, usually above a specified DBH.
- a trail monitoring a few individuals of certain key species.

Both Chapman et al. (1994b) and Blake et al. (1990) have compared the accuracy of the above methods. There exists no 'true' measure of community wide fruit abundance with which to compare the results of the different methods. However, Chapman et al. (1994b) found that the results of a transect system and a trail system closely correlated, whereas the results from the fruit traps did not correlate with either of the other methods. They concluded that the selection between a systematic area-based methodology or a non-systematic trail including only key species will depend upon the amount of time an investigator has available for sampling and existing knowledge of key species for inclusion in the trail. Blake et al. (1990) also concluded that area-based sampling techniques will provide the most accurate quantitative information and are therefore the most useful for inter-site comparisons.

Both studies state that if only key species are monitored, knowledge of their densities will be necessary in order to extrapolate results to food availability in the study area. Whichever method is chosen, accuracy will increase as a greater proportion of the study animals' home range is sampled. It is important that a representative sample of all vegetation types occurring within the study animals' range are included in the area sampled. Hemingway & Overdorff (1999), also stressed that phenological sampling should be as wide as possible because of great individual variation in reproductive activity. It is also important that where possible methodologies between sites should be standardised (Malenky et al., 1993). Within these two methods it is then possible to assign abundance scores for each visible phenophase on each tree or simply record the tree as exhibiting or not exhibiting each phenophase. Chapman et al. (1992) compared the accuracy and precision of different methods to estimate fruit abundance on a tree; a measure of the physical size of a fruit bearing tree, using either the diameter at breast height, (DBH), or crown volume; or a visual estimation of the amount of fruit on a tree. DBH was the most consistently accurate method and exhibited low levels of inter-observer variability. However, visual estimation is the only method by which individual tree variation in crop size over time can be measured.

For this study I chose a non-systematic trail regime for monitoring the phenology of known chimpanzee food species and a systematic area-based method to record the fruit availability of all forest species, referred to from now on as the 'community-wide' sample. DBH was used as a measure of patch size and the abundance of each phenological state; buds, young and mature leaves, flowers, unripe, half-ripe and ripe fruit, was recorded using a scale of 0-4. The correlation between these two methods of estimating food availability will be discussed.

After the initial setting up of the phenology trail, all phenology data were collected by my field assistant Julius Kyamanya. Julius has worked with the Budongo Forest Project since 1991 and has previously collected phenological data for other studies. His previous experience was essential for accurately identifying the differing phenological phases of each species.

Phenology Trail Of Known Chimpanzee Food Species

Food availability in the study area was measured systematically every two weeks for a total of 16 months from September 1997 to December 1998 (35 phenology samples). A total of 378 individual trees representing 26 species were monitored (representing 13 families) (see Table 4.1). The 26 species were selected as being important in the diet of the chimpanzees. This selection was based on information from previous studies at Budongo (Reynolds, 1963, 1965, 1992; Sugiyama, 1968; Bakuneeta, pers. comm.) and also through discussion with the field assistants to identify species which were thought to be important at different times of the year or which seemed to be particularly sought after by the chimpanzees (most of the field assistants have worked with this community of chimpanzees since 1990). Also included were species which are important chimpanzee food species at other sites, notably Kibale Forest, Uganda, and also present in Budongo, even if the species is not yet known to be eaten by the Sonso community (Wrangham et al., 1992).

A phenology trail, approximately 10km in length, was established within the chimpanzee community range. Initially, a stratified random sample of twelve 200m x 10m transects were located within the existing trail system. These transects covered all vegetation types. All individual trees of the selected species (see Table 4.1) which had a DBH greater than 10cm were included. It was thought that trees greater than 10cm DBH would be mature enough to fruit and strong enough to support an adult chimpanzee. These transects were linked together by a trail and any species which were under-represented on the transects were added along the trail. Numbers were adjusted to include 20-25 individuals of each species, however for the rarer species this number was reduced to 10 and in some cases it was not possible to locate even 10 individuals. Once selected, each tree was marked with an aluminium tag for future identification. The phenology trail, once established, took 3 mornings to sample. The percentage canopy cover for each tree was given a phenology score, estimated on a scale of 0-4 (including 0.5 intervals), for mature leaves, young leaves, leaf buds, unripe fruit, ripe-fruit, and flowers. The category 'half-ripe' fruit was added because in some species, notably some fig species, it was possible to identify different stages of the fruit ripening process. In order to provide detail this has been left as a separate

class of fruit. The chimpanzees would treat it more like ripe fruit than unripe, however given a choice they prefer ripe fruit.

Table 4.1 List of Trees and Numbers Included on the Phenology Trail of Known Chimpanzee Food Species.

Family	Species	Code	Number on Trail
Anacardiaceae	*Lannea welwitschii*	LW	4
	Pseudospondias microcarpa	PSM	13
Boraginaceae	*Cordia milleni*	COM	22
Cecropiaceae	*Myrianthus holstii*	MYH	20
Euphorbiaceae	*Croton sylvaticus*	CSY	20
Leguminosae	*Cynometra alexandri*	CYA	25
	Mildbraediodendron excelsum	MIE	5
Meliaceae	*Khaya anthotheca*	KA	20
Moraceae	*Broussonetia papyrifera*	BPY	21
	Ficus barteri	FB	2
	Ficus exasperata	FE	20
	Ficus mucuso	FM	9
	Ficus polita	FP	6
	Ficus sansibarica	FSA	4
	Ficus saussureana	FSS	10
	Ficus sur	FSU	21
	Ficus vallis-choudae	FVL	2
	Ficus variifolia	FVR	21
	Milicia excelsa	MEX	16
	Morus lactea	MOL	10
Oleaceae	*Olea welwitschii*	OLW	3
Rhamnaceae	*Maesopsis eminii*	ME	16
Sapotaceae	*Chrysophyllum albidum*	CAL	18
Ulmaceae	*Celtis durandi*	CDU	20
	Celtis mildbraedii	CMI	24
	Celtis zenkeri	CZE	24

Density Transects

As the trees along the phenology trail were selected in a biased manner, it was necessary to correct for differences in density between species (Chapman et al., 1994b). In order to do this, 24 additional transects 200m x 10m were established. Along these transects the number of chimpanzee food trees was counted and their DBH measured. Some of the rarer species, namely figs, were not encountered. A total of 825 trees were sampled. From these data, average DBH values were calculated in order to calculate patch size by species.

Table 4.2 Number Of Chimpanzee Food Species Along Density Transects.

Tree Species	no. on transects	mean DBH
BPY	2	32.5
CAL	6	39.83
CDU	106	37.36
CMI	250	20.44
COM	15	47.40
CSY	38	34.97
CYA	64	65.94
CZE	99	26.84
FE	21	39.95
FM	3	23.00
FPO	1	STRANGLER
FSU	21	36.81
FVR	11	33.64
KA	76	36.67
LW	40	40
ME	27	63.59
MEX	1	21
MIE	2	74
MOL	3	25.67
MYH	21	19.14
OLW	3	42.33
PSM	3	31.00

Forest community-wide fruiting patterns

In addition, as the phenology trail was walked, all trees within the phenology sample area (10000mx10m) which had fruit, (unripe, *half-ripe* and ripe), were identified and a phenology score and DBH recorded. This included all species present in the forest and should therefore give an index of forest community-wide fruit abundance. (see Appendix B.4 for a list of all species recorded from community-wide phenology sampling).

Seasonal patterns in food availability were investigated by classifying phenological sample periods into four seasons based on rainfall patterns. (see chapter 2).

4.4 Analyses

Phenology Trail Of Known Chimpanzee Foods.

Estimates of food availability were calculated using two slightly different methods in order to assess the validity of visual measurements of food abundance.

Method A

By summing the scores of each phenological state of each tree of each species, from each bi-weekly sample. From these totals an average score was calculated for each species by dividing by the number of trees sampled. This value was then multiplied by the density of each species and then multiplied again by the average patch size (DBH) of each species. The results are expressed as an index of 100, where the period with the highest value equals 100.

Method B

As above except the score for each phenological state was ignored and instead the tree was recorded as simply exhibiting, (+), or not exhibiting, (-), each phenological state.

Forest community-wide fruiting patterns

These data were also analysed using the two methods outlined above. Data from the tagged trees along the phenology trail and all the additional fruiting trees were combined for the analyses. For these analyses the phenology trail was considered as one transect (10 x 10 000m). Therefore, it was not necessary to correct for density values. The DBH value used was that of the actual fruiting trees. The DBH of fruiting trees was estimated visually, using size classes of 10 cm i.e. <10cm, >10-<20, >20-<30 etc.

Statistical Analyses

Non-parametric tests were used. Kendal Concordance Coefficient was used to test for synchrony between the differing phenological states. Spearman Rank correlation statistical tests were applied to test for correlations between results using abundance

scores and DBH, the number of species exhibiting each phenological state and measures of abundance, and correlations between the phenological patterns of known chimpanzee foods and forest community-wide phenology. Kruskal-Wallis statistical tests were used to examine correlations between phenology data and season.

4.5 Results

Comparison Of The Two Different Methods For Estimating Food Availability.

a) Chimpanzee Food Species Availability

To test any differences between phenology information analysed by method A (using a combination of abundance scores and DBH values of each fruiting tree to assess fruit abundance) and Method B (using only the DBH value of each fruiting tree to assess fruit abundance) the data were analysed using the non-parametric Spearman Rank correlation test. The results using the two methods were significantly correlated for all phenological states, (*buds* r_s = 0.835, $p<0.001$; *young leaves* r_s = 0.874, $p<0.001$; *mature leaves* r_s = 0.847, $p<0.001$; *unripe fruit* r_s = 0.861, $p<0.001$; *half-ripe fruit* r_s = 0.886, $p<0.001$; *ripe fruit* r_s 0.993, $p<0.001$; *flowers* r_s = 0.773, $p<0.001$), indicating that it is sufficient to simply record the presence or absence of a phenophase on individual trees in order to assess changes in food availability. However, the magnitude of the peaks and troughs of abundance and scarcity were more pronounced in the analyses using scores for the availability of each phenological state (method A). It is considered that the amplitude of the periods of food abundance and scarcity are important to the primary consumers. Therefore, only data assessing the abundance of phenophases on individual trees, Method A, are analysed further and shown in figures 4.1 - 4.9. (See Appendix B.1 for data obtained using method B).

b) Forest community fruit availability,

Similarly, differences in the measures of availability of unripe, half-ripe and ripe fruit using methods A and B were tested using the Spearman Rank correlation test. Again the two measures were significantly correlated (*unripe fruit* r_s = 0.772, $p<0.001$; *half-*

ripe fruit $r_s = 0.939$, $p<0.001$; *ripe fruit* $r_s = 0.887$, $p<0.001$). On visual examination the charts from both the analyses had the same general pattern with no notable differences in the magnitude of the peaks and troughs. However, for consistency with the chimpanzee food species data, only data analysed using method A are presented. Data using Method B are in Appendix B.2.

Phenology Patterns of Food Availability

Using the Kendall's Coefficient of Concordance the phenological abundance patterns of buds, young leaves, mature leaves, flowers, unripe fruit, half-ripe fruit, ripe fruit for chimpanzee food species were found to exhibit synchrony in their phenological patterns of production, ($W= 0.370$, $p<0.01$), see Fig 4.9. Likewise, number of species exhibiting each phenological state during each period was correlated ($W = 0.317$, $p<0.01$), see Fig 4.14 a & b.

A detailed examination follows of the temporal patterns and seasonality of each phenophase for the known chimpanzee food species, and also the fruiting patterns of the forest community-wide (see Fig 4.1-4.13, rainfall is shown as a line on all figures.)

Buds: bud production occurred throughout the year with a peak in April 98 (see Fig 4.1). This coincided with the onset of rainy season(1), (see Chap 2). A smaller peak was also observed in Sep 98 at the start of rainy season(2). A Kruskal-Wallis test showed significant seasonal differences in the availability of buds ($K = 10.64$, $p<0.05$). The number of species producing buds, (Fig 4.14), was significantly correlated to the phenological abundance scores, $r_s = 0.386$, $p<0.05$).

Young Leaves: young leaf production occurred throughout the year (Fig 4.2). There was a significant seasonal difference in the production of young leaves ($K = 11.221$, $p<0.05$). There was a bi-modal pattern of peaks of abundance starting at the beginning of dry season(1), then falling during the dry season and then peaking again at the start of rainy season(1). Dry season(2) corresponded to a reduction in the

Fig 4.1 Availability Of **Buds** Along The Chimpanzee Food Species Phenology Trail (Bars), Rainfall (Line).

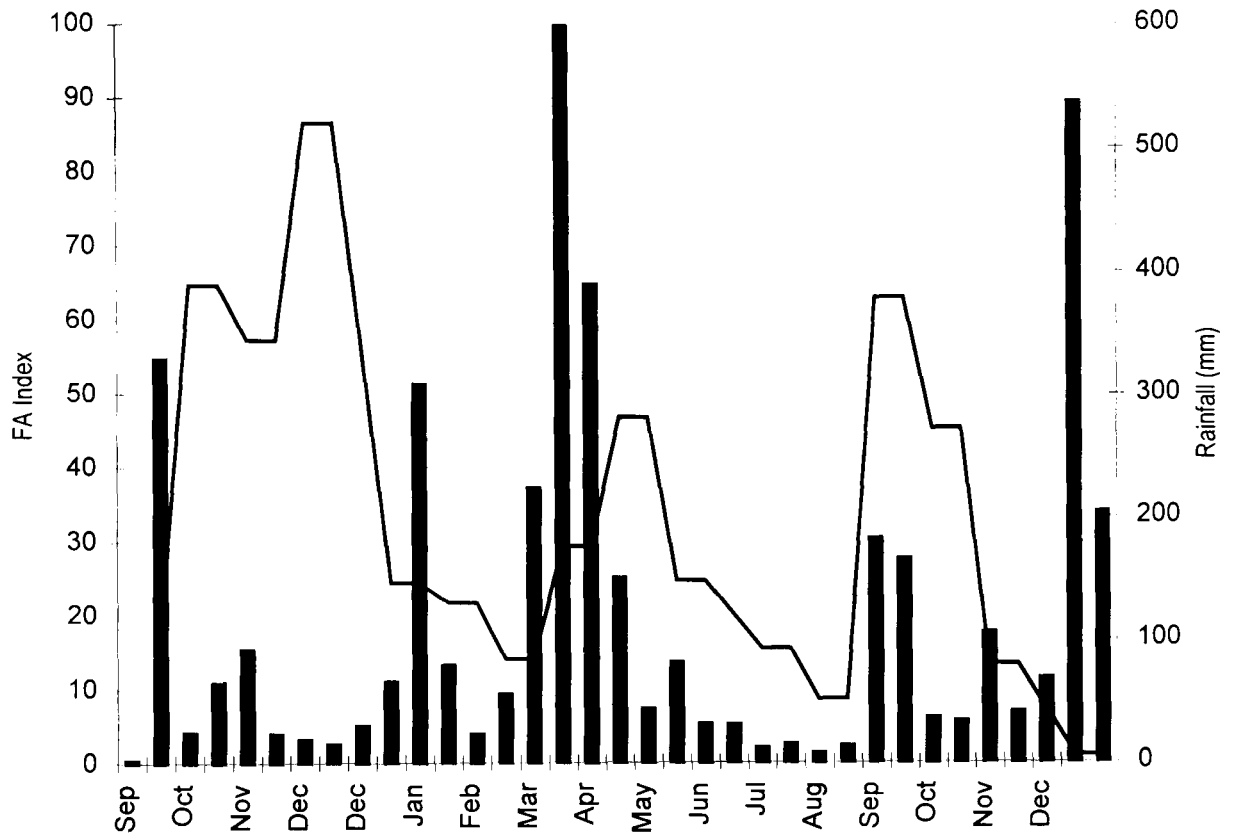
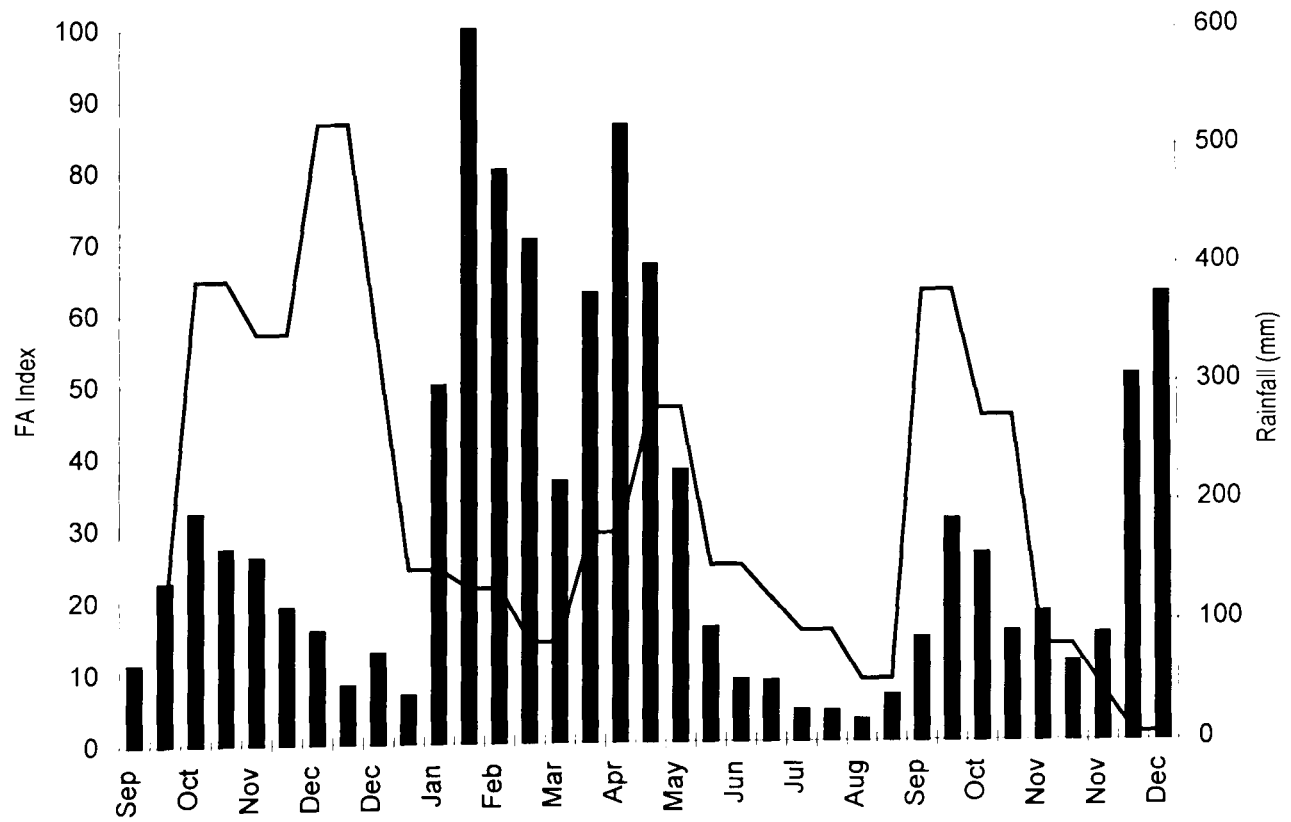


Fig 4.2 The Availability Of **Young Leaves** Along The Chimpanzee Food Species Phenology Trail (Bars), Rainfall (Line).



production of young leaves. The number of species producing young leaves, (Fig 4.2), was correlated with the abundance measures of young leaves (r_s = 0.710, p<0.01).

Mature Leaves: mature leaves were abundant throughout the year with a minimum occurring dry season(1), Feb-April 98 and in Dec 98 (Fig 4.3). This correlated with a decrease in rainfall and an observed distinct shedding of mature leaves. No obvious shedding event occurred during dry season(2). The availability of mature leaves was significantly negatively correlated with the production of buds (r_s = -0.517, p<0.01), young leaves (r_s = -0.855, p<0.01) and flowers (r_s = -0.440, p<0.01). There was a significant difference in the seasonal production of mature leaves (K = 16.484, p<0.01). The only months when the number of species with mature leaves dropped from the maximum were March and December 98, both times during dry season(1). The number of species with mature leaves (Fig 4.14) was not correlated with the measures of abundance of mature leaves. There were no significant seasonal differences in the number of species with mature leaves. This is probably because most trees always had at least a few mature leaves, even during the flushing of new leaves.

Flowers: flowers were produced in all months (Fig 4.4). Flowering peaks were during rainy season(2) and dry season(1) of each year. The major peak was during dry season(1) each year. As expected, peaks in flower production were followed by peaks in unripe fruit production. There was a significant correlation between the number of species producing flowers, (4.14) and their availability (r_s = 0.440, p<0.01). There were no significant seasonal differences, based on rainfall patterns, in either the availability or the number of species producing flowers (K = 7.387, n.s.).

Unripe Fruit: unripe fruit was available throughout the year with a major peak in April 98 (Fig 4.5). The majority of this peak was attributable to a single, abundant species, *C. durandi*, (see Table 4.2). When this species was removed from the analyses the pattern changes. Unripe fruit is then seen to be abundant during

Fig 4.3 The Availability Of **Mature Leaves** Along The Chimpanzee Food Species Phenology Trail (Bars), Rainfall (Line).

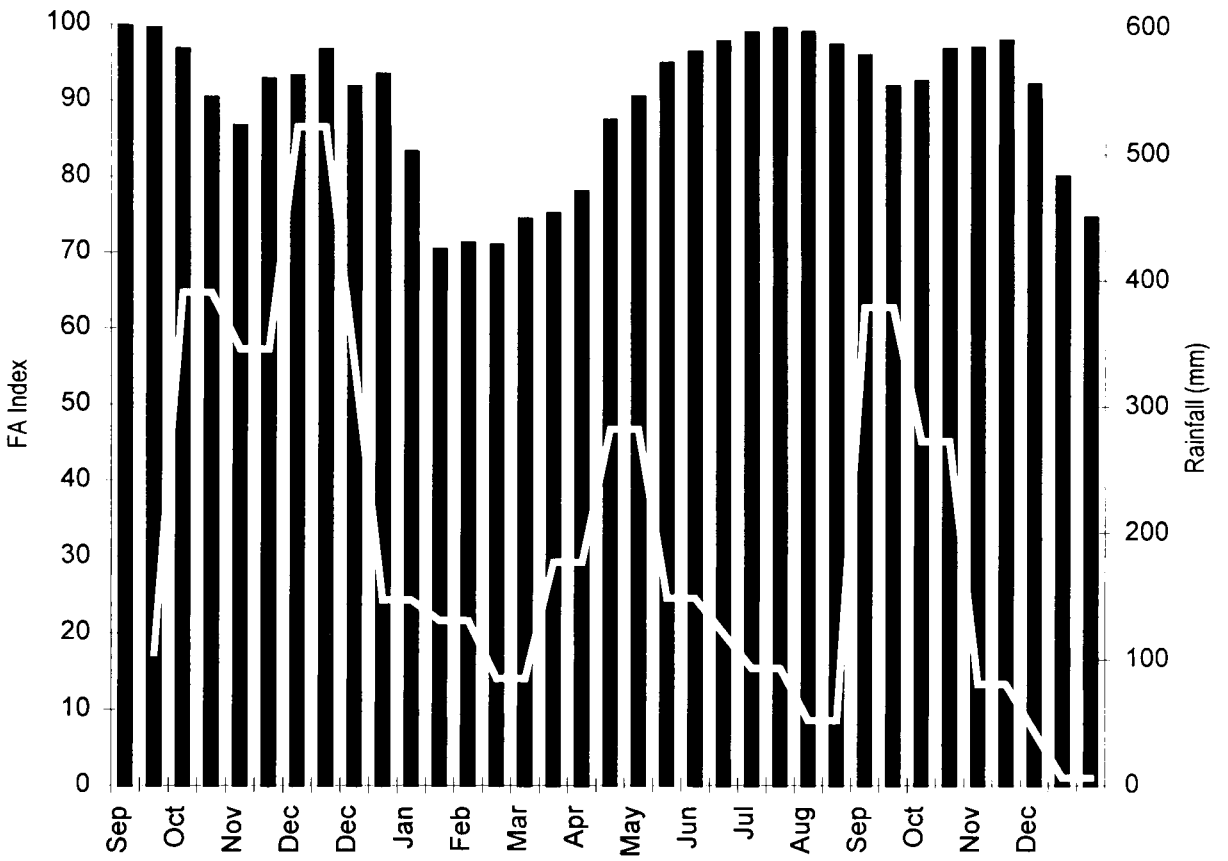


Fig 4.4 The Availability Of **Flowers** Along The Chimpanzee Food Species Phenology Trail (Bars), Rainfall (Line).

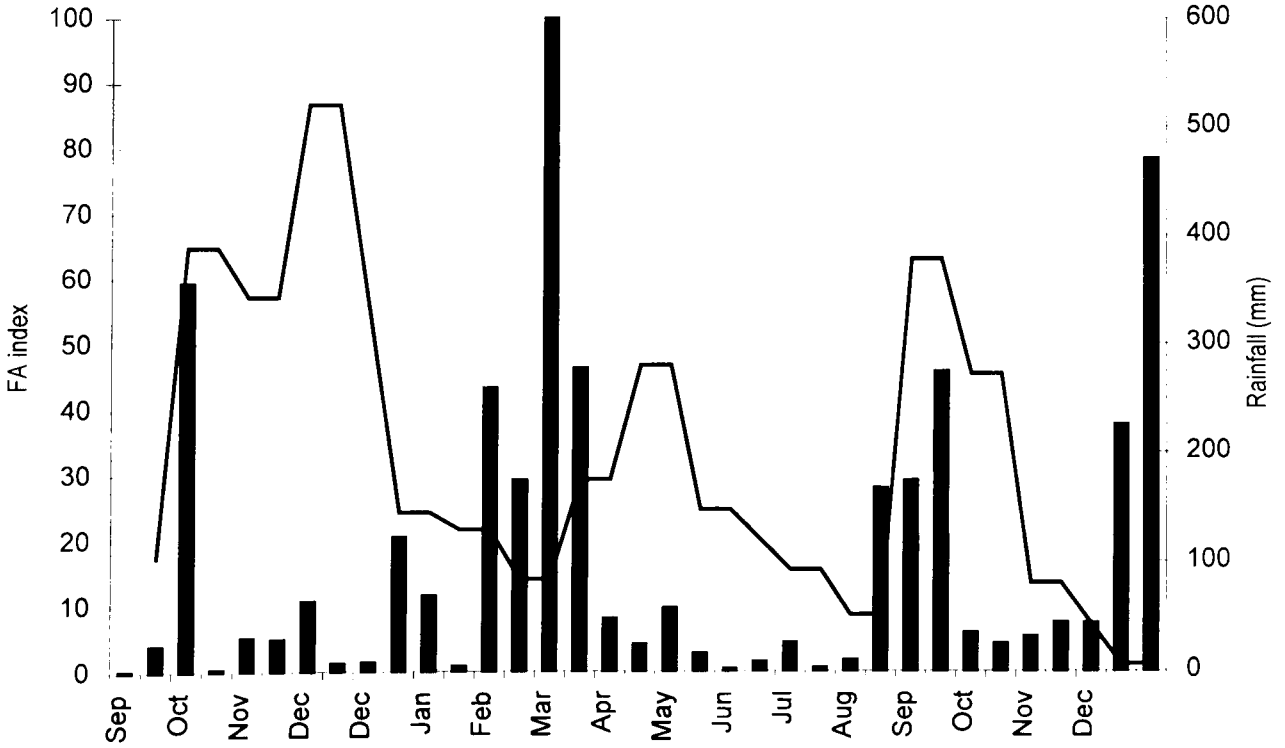


Fig 4.5 The Availability Of **Unripe Fruits** Along The Chimpanzee Food Species Phenology Trail (*Celtis durandii* (CDU) open bars, all other species solid bars), Rainfall (Line).

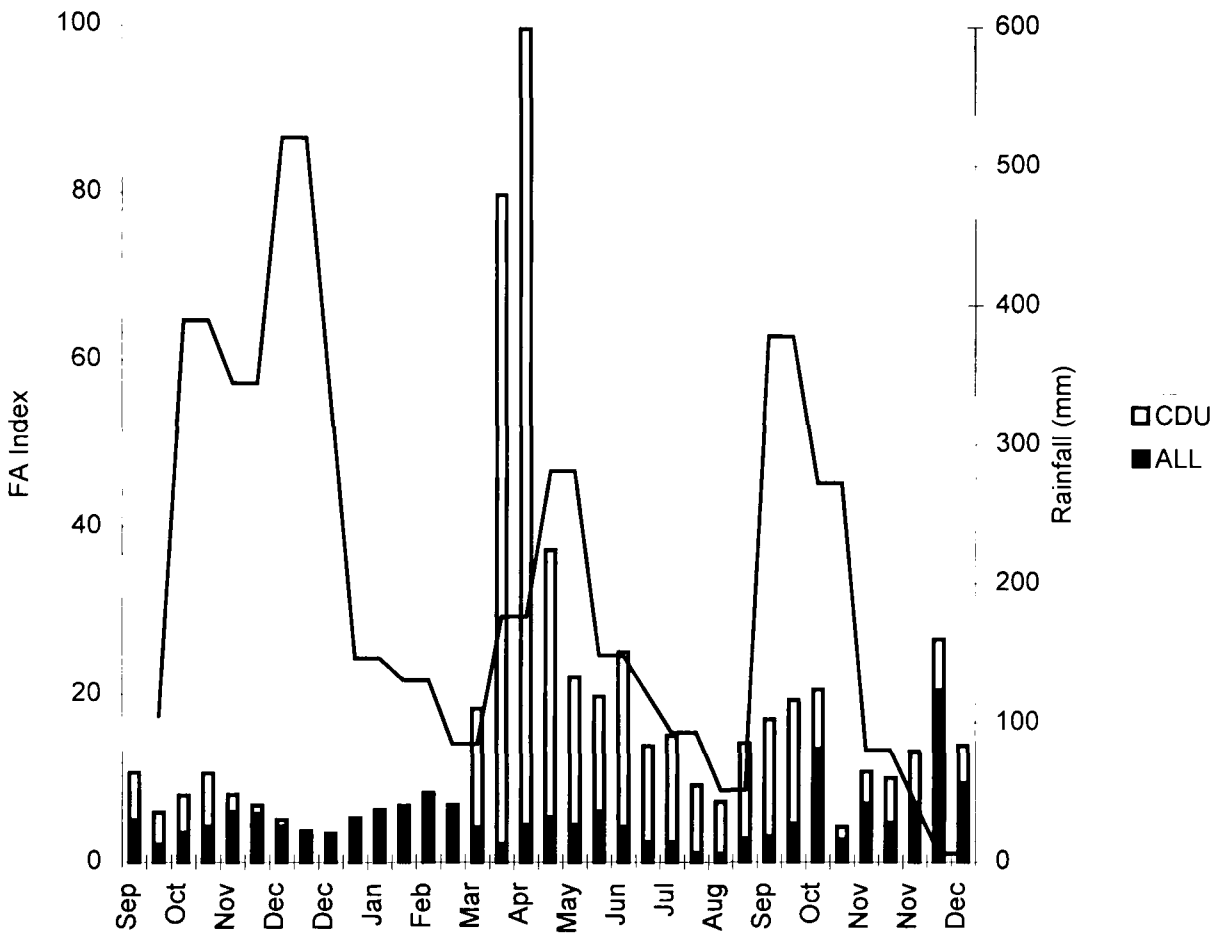
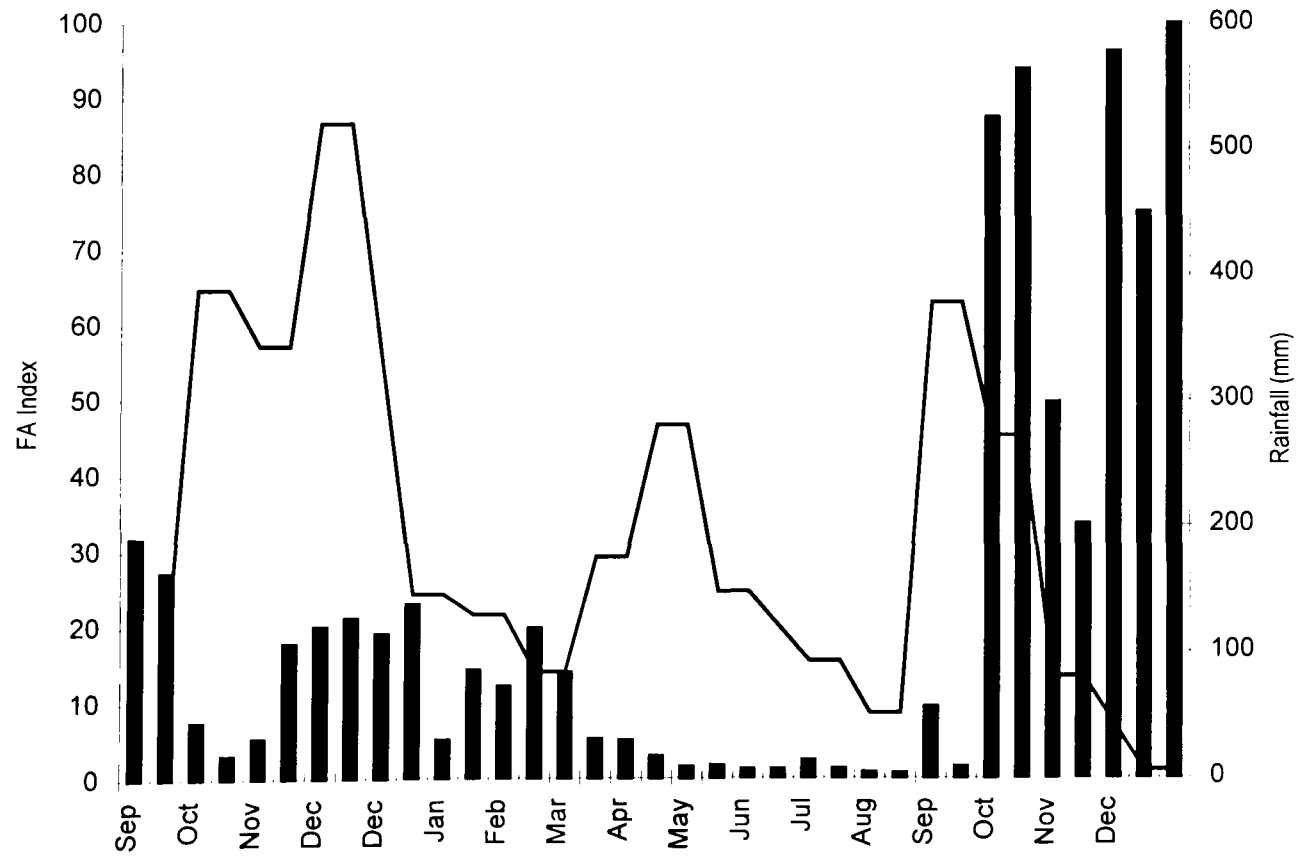


Fig 4.6 The Availability Of **Half-Ripe Fruit** Along The Chimpanzee Food Species Phenology Trail (Bars), Rainfall (Line).



the rainy season(2) and the subsequent dry season(1) (i.e. throughout Oct 97-Mar 98). There was then a drop in availability during late March to late April. This coincided with a peak in the production of ripe fruit. Further troughs in the availability of unripe fruit occurred during Aug and Oct 98 which did not coincide with the production of ripe fruit. The trough in Aug may have been caused by a reduction in rainfall, whereas the trough in Oct may have been a result of an increase in the availability of half-ripe fruit. There was a significant seasonal difference in the abundance of unripe fruit (K= 12.832, $p<0.01$). There was no significant correlation between the availability of unripe fruit and the number of species producing unripe fruit (r_s = 0.264, ns). There was a significant difference across seasons in the number of species bearing unripe fruit (K= 13.208, $p<0.01$). Peaks in the number of species bearing unripe fruit generally coincided with the rainy seasons (Fig 4.14). Troughs again correspond with either dry seasons or an increase in half-ripe fruit production.

Half-Ripe Fruit: half-ripe fruit was available every month, with peaks occurring in Sep 97, Nov 97-Jan 98, Feb-Mar 98, and Oct-Dec 98 (Fig 4.6). The most dramatic pattern was that there was a greater amount of half-ripe fruit available towards the end of 1998 than there was available at the same time of year in 1997. Periods of low half-ripe fruit availability were from May 98 until the end of Aug 1998. There was a seasonal difference in the availability of half-ripe fruit (K = 14.388, $p<0.01$). The number of species bearing half-ripe fruit was significantly correlated to the abundance scores (r_s = 0.408, $p<0.05$).

Ripe Fruit: a single-species, *Croton sylvaticus*, produced an abundance of ripe fruit during Sep and Oct each year (Fig 4.7). Otherwise, the general peak in ripe fruit abundance occurred in Mar 98. This coincides with the end of dry season(1). No ripe fruit was recorded during the phenology sample periods in Oct 97 and June 98. However, there were no significant seasonal differences in the availability of ripe fruit (K= 0.279, ns). The number of species producing ripe fruit (Fig 4.14) was significantly correlated with the phenological abundance scores (r_s = 0.426, $p<0.05$).

Fig 4.7 The Availability Of **Ripe Fruit** Along The Chimpanzee Food Species Phenology Trail (Bars), Rainfall (Line).

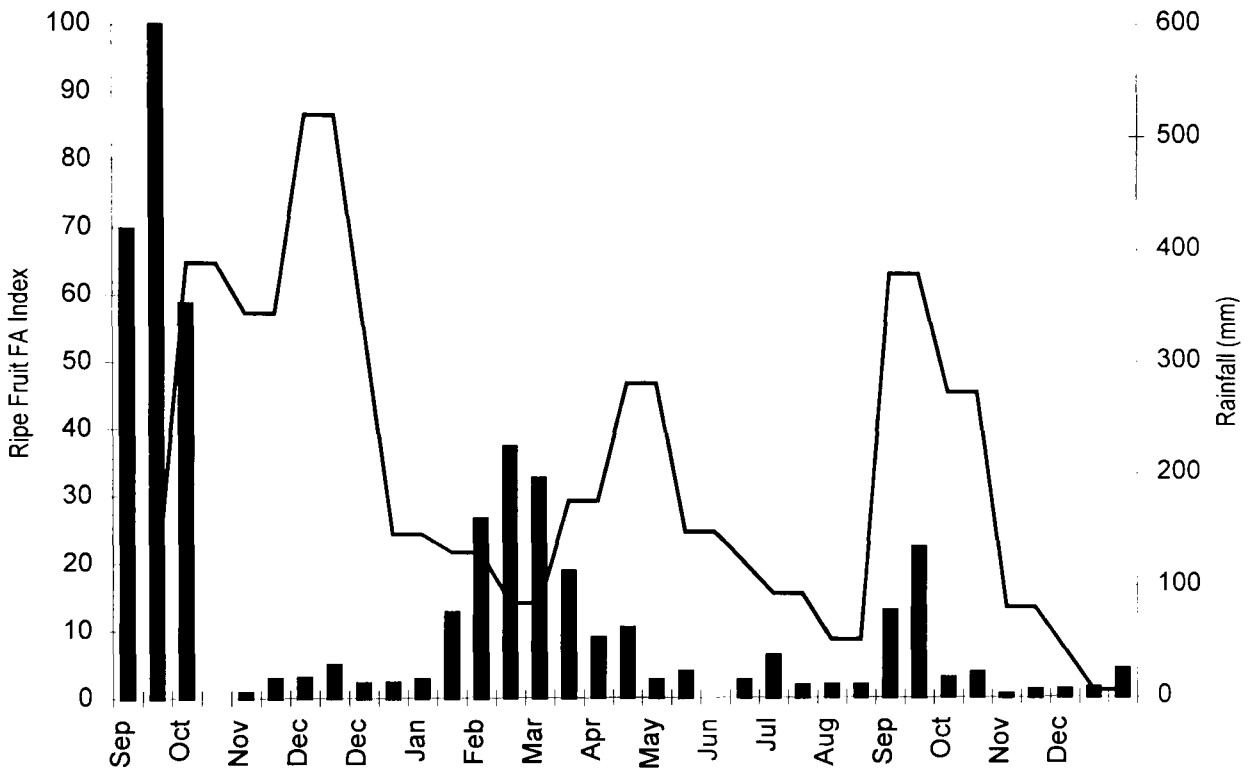


Fig 4.8 The Total Availability Of **All Fruit** Along The Chimpanzee Food Species Phenology Trail (Bars), Rainfall (Line).

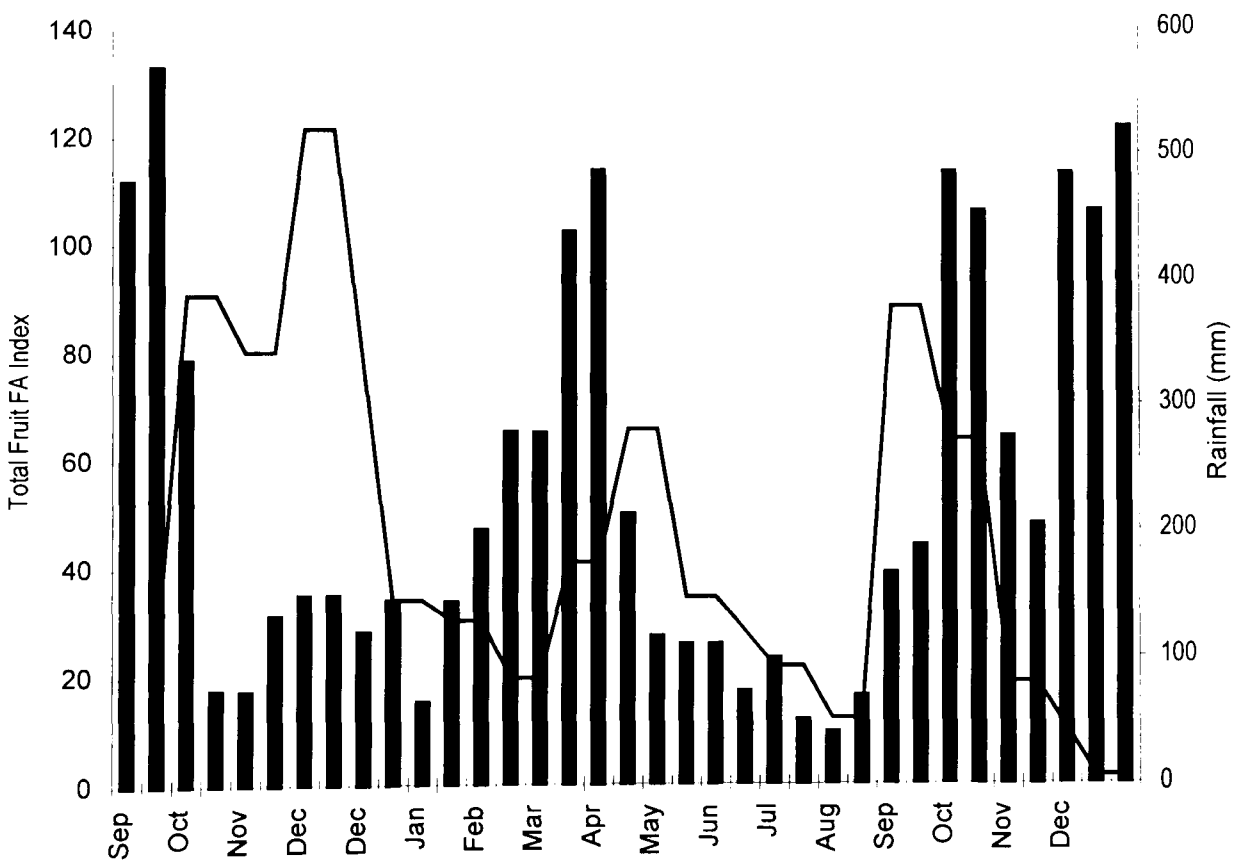
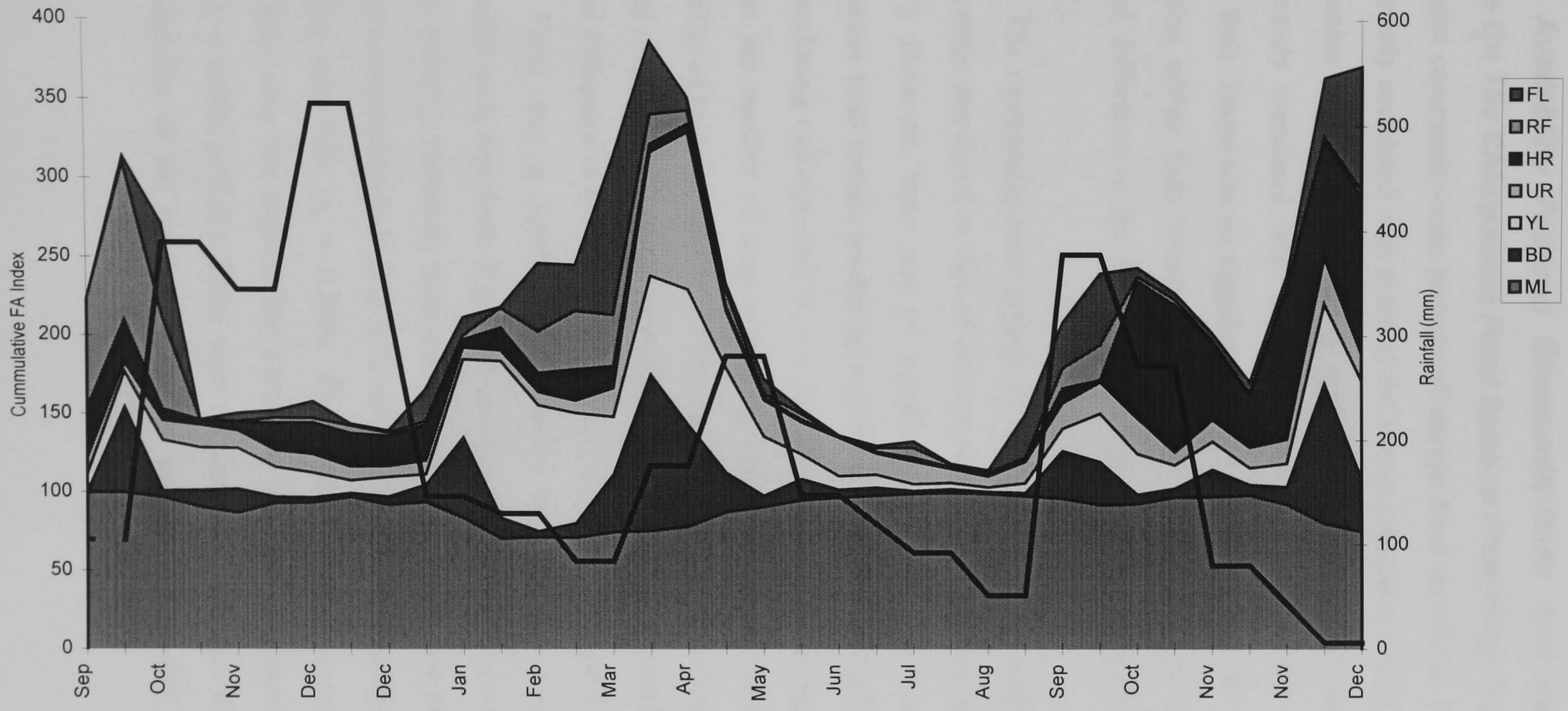


Fig 4.9 Overview of Figures 4.1-4.8: A Visual Representation of the Combined Food Availability Indices (FA) from the Phenology Trail. (FL= flowers, RF= ripe fruit, HR= half-ripe fruit, UR= unripe fruit, YL= young leaves, BD= buds, ML= mature leaves)



There was also a significant seasonal difference in the number of species producing ripe fruit ($K = 0.034$, $p<0.05$).

Food Availability Patterns Community-Wide And Comparison With Those On The Chimpanzee Food Species Phenology Trail.

The forest community-wide patterns of **unripe fruit** abundance (Fig 4.10) were not significantly correlated with those of the known chimpanzee food species. However, the number of species producing unripe fruit community-wide (Fig 4.13) was significantly correlated with the number of chimpanzee food species producing unripe fruit. There was no significant seasonal difference in the number of species producing unripe fruit community-wide (K= 1.814, ns). However, there was a seasonal difference in the abundance of unripe fruit community-wide (K=15.740, $p<0.01$).

The community-wide pattern of **half-ripe fruit** abundance (Fig 4.11) was significantly correlated to that of the known chimpanzee food species ($r_s = 0.599$, $p<0.01$). However, there was no significant correlation between the number of chimpanzee food species producing half-ripe fruit (Fig 4.13) and those community-wide producing half-ripe fruit ($r_s = 0.167$, ns). There was no significant correlation between the number of trees producing half-ripe fruit community-wide and the availability of half-ripe fruit (r_s =0.296, ns). There was a significant difference in the seasonal abundance of community-wide half-ripe fruit ($K = 10.699$, $p<0.05$), but no seasonal difference in the number of species producing half-ripe fruit ($K = 4.611$, ns).

There was a significant correlation between the availability of forest community-wide **ripe fruit** (Fig 4.12) and that of known chimpanzee food species ($r_s = 0.540$, $p<0.01$). However, there was no significant correlation between the number of species community-wide (Fig 4.13) and those of known chimpanzee food species producing ripe fruit ($r_s = 0.245$). The number of species producing ripe fruit community-wide was significantly correlated with the community-wide abundance score ($r_s = 0.546$, $p<0.01$). There were no significant seasonal differences in either the abundance or the number of species producing ripe fruit community-wide.

Fig 4.10 The Availability Of **Unripe Fruit** In The Forest Community (Bars), Rainfall, (Line).

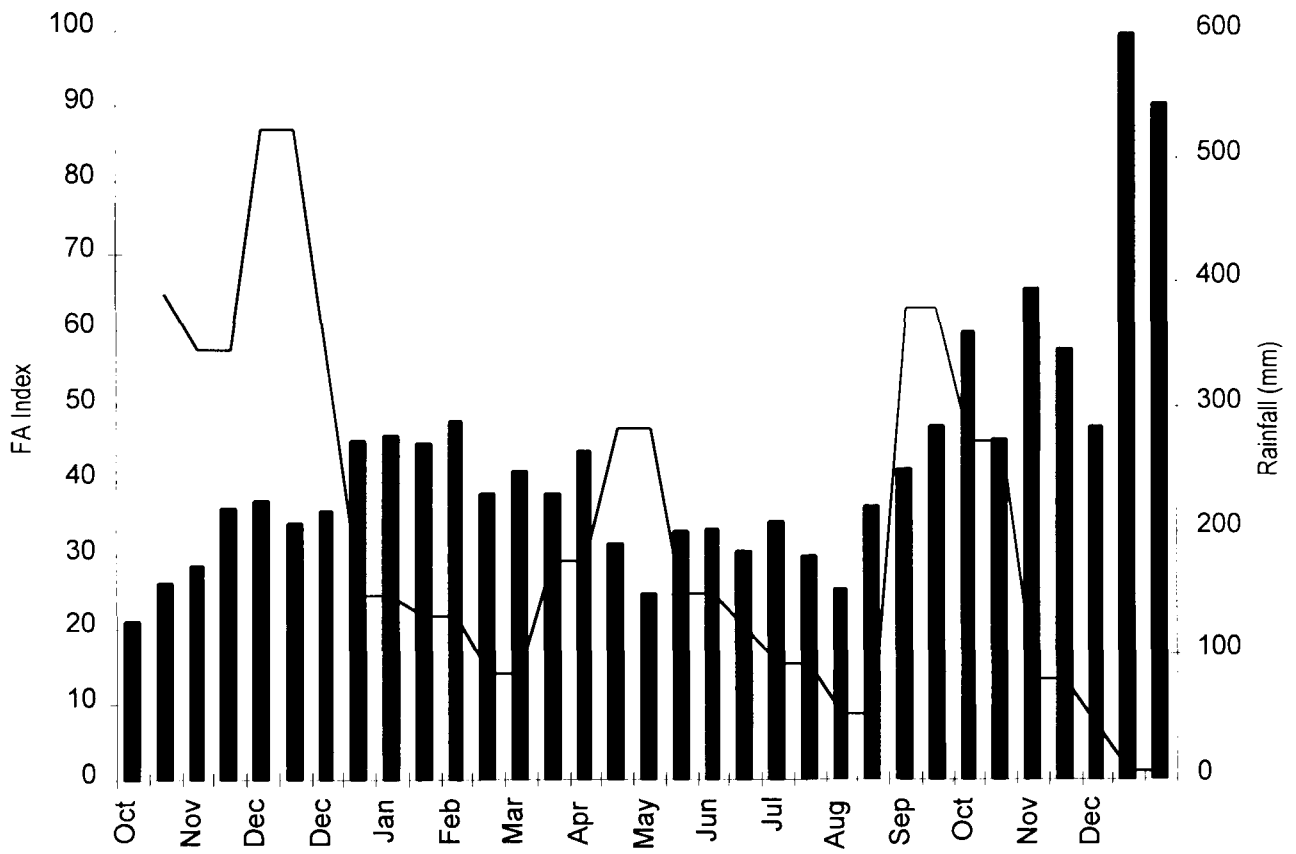


Fig 4.11 The Availability Of **Half-ripe Fruit** In The Forest Community (Bars), Rainfall, (Line).

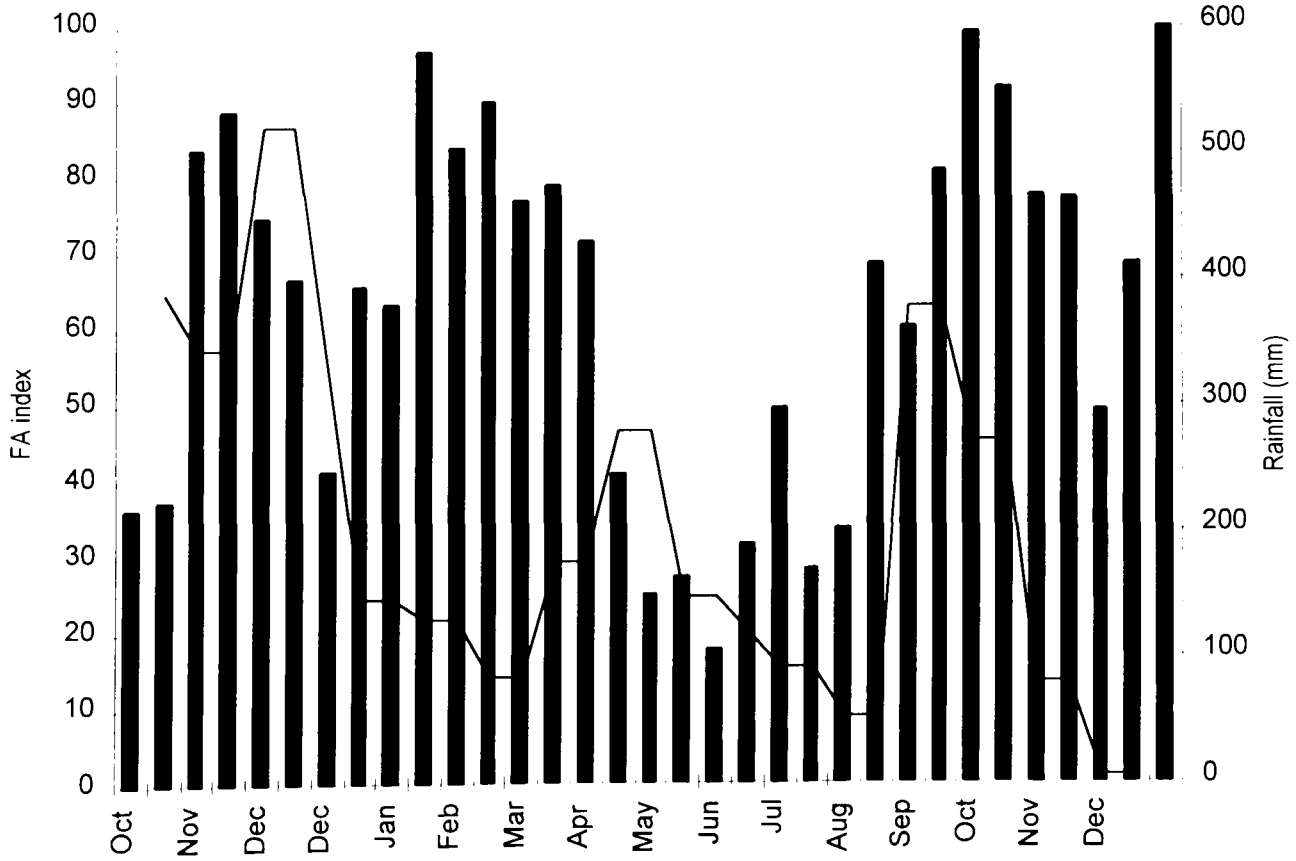


Fig 4.12 The Availability Of **Ripe Fruit** In The Forest Community (Bars), Rainfall, (Line).

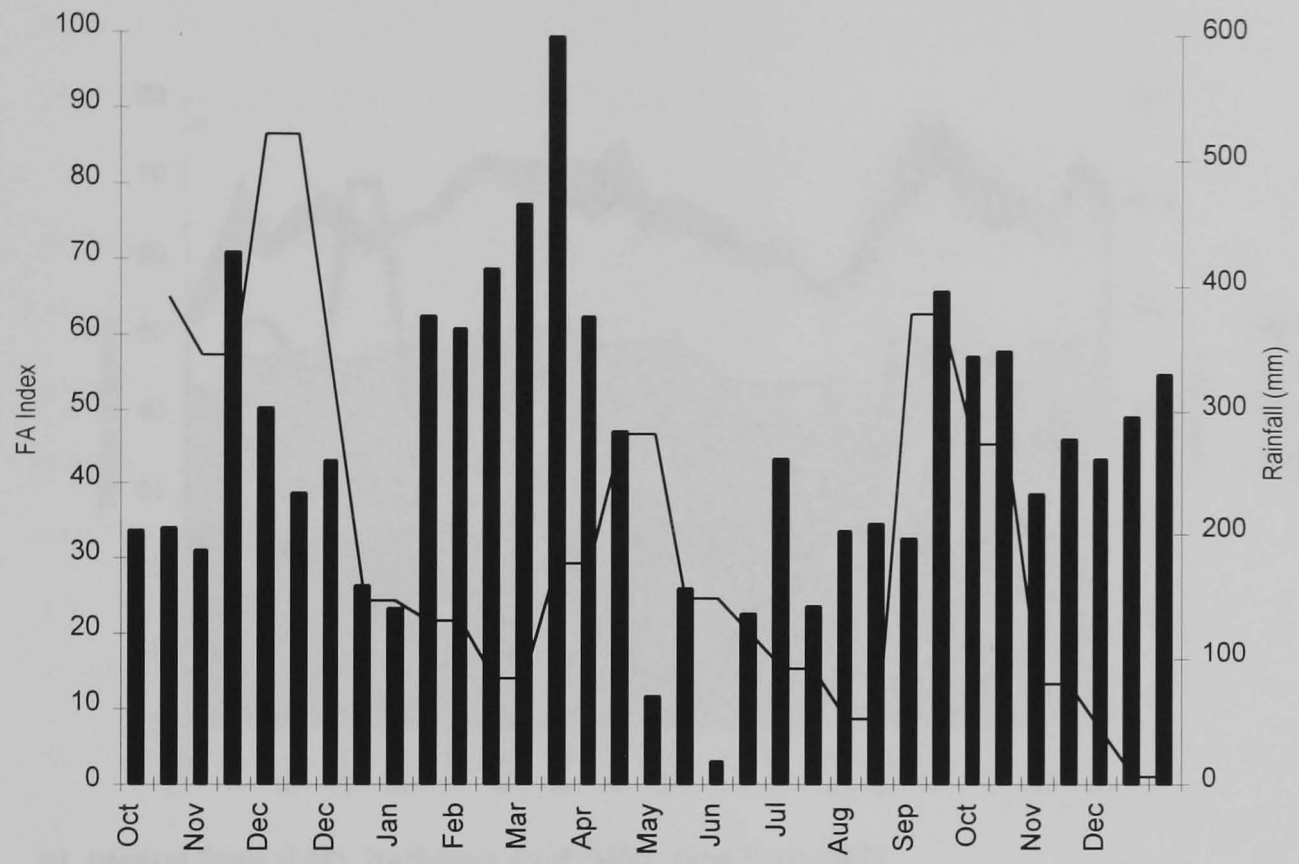


Fig 4.13 The Number Of Species In The Forest Community Producing Unripe Fruit (UR), Half-Ripe Fruit (HR) and Ripe Fruit (RF).

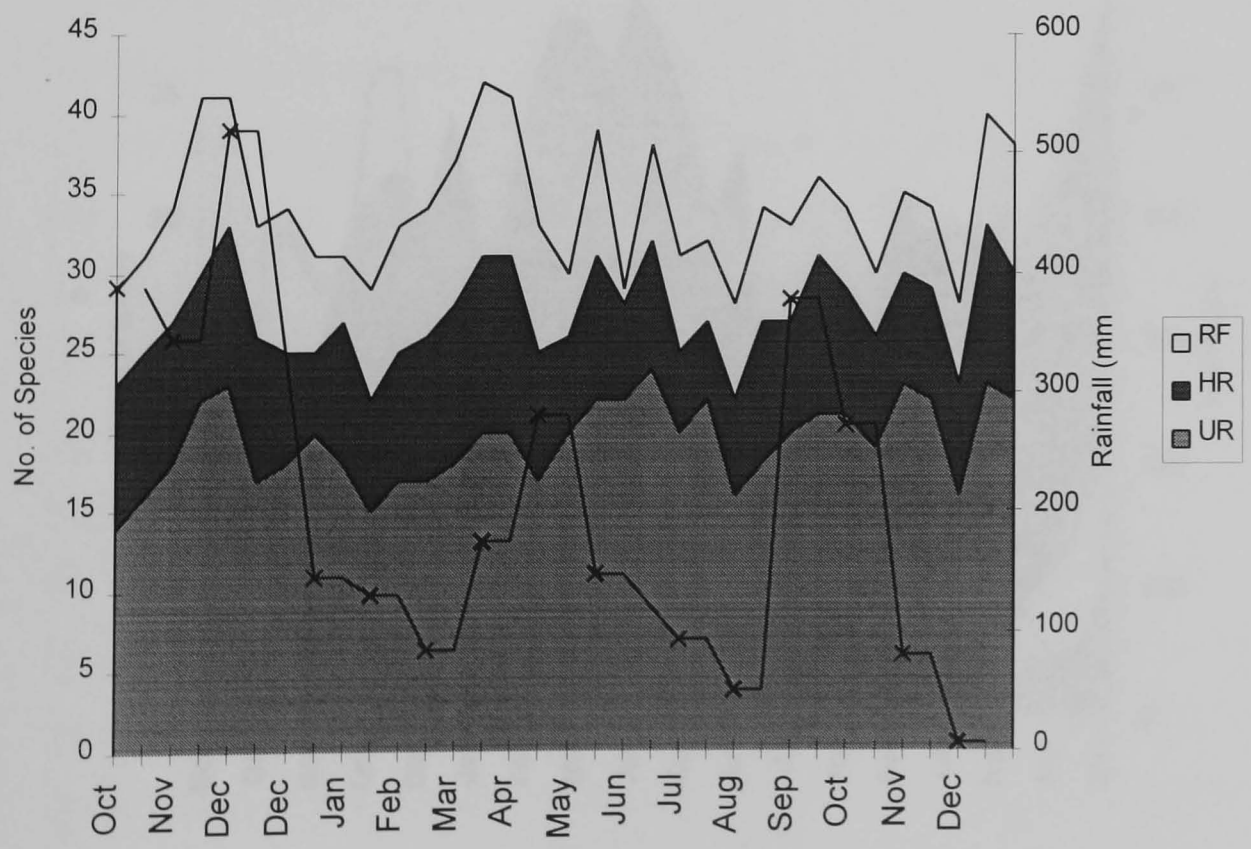
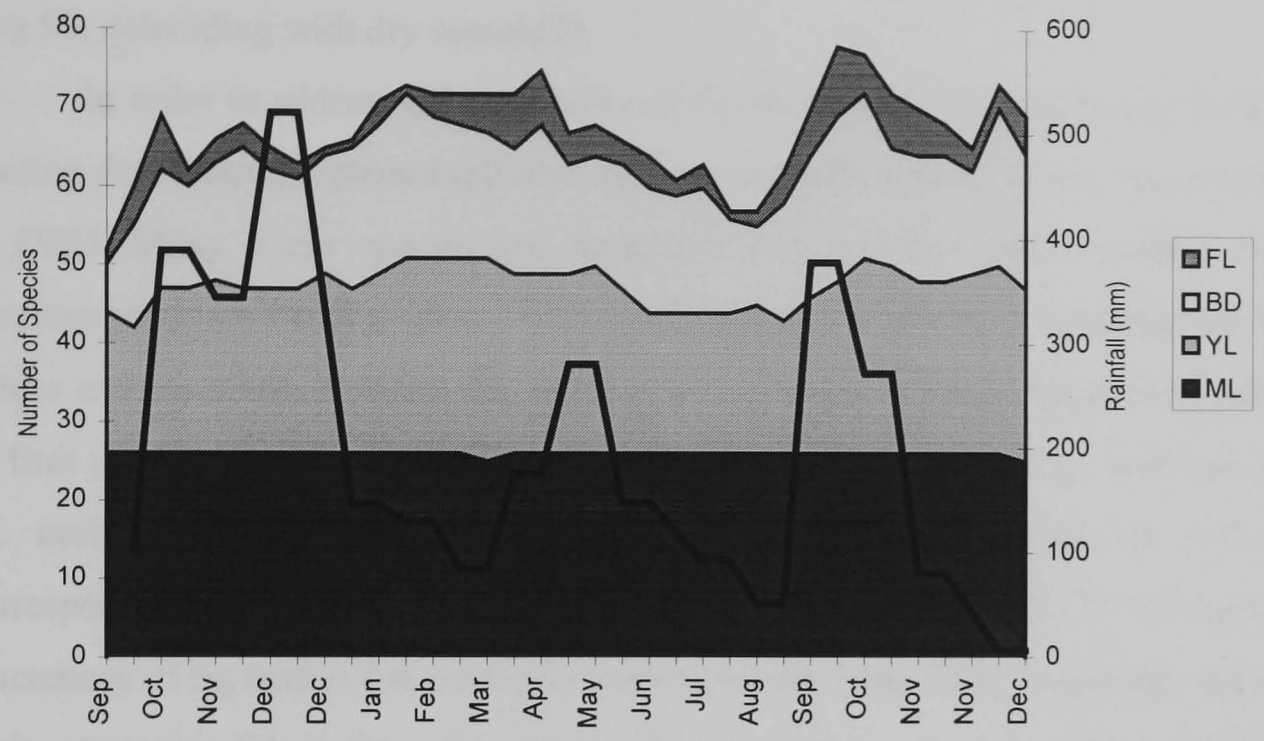
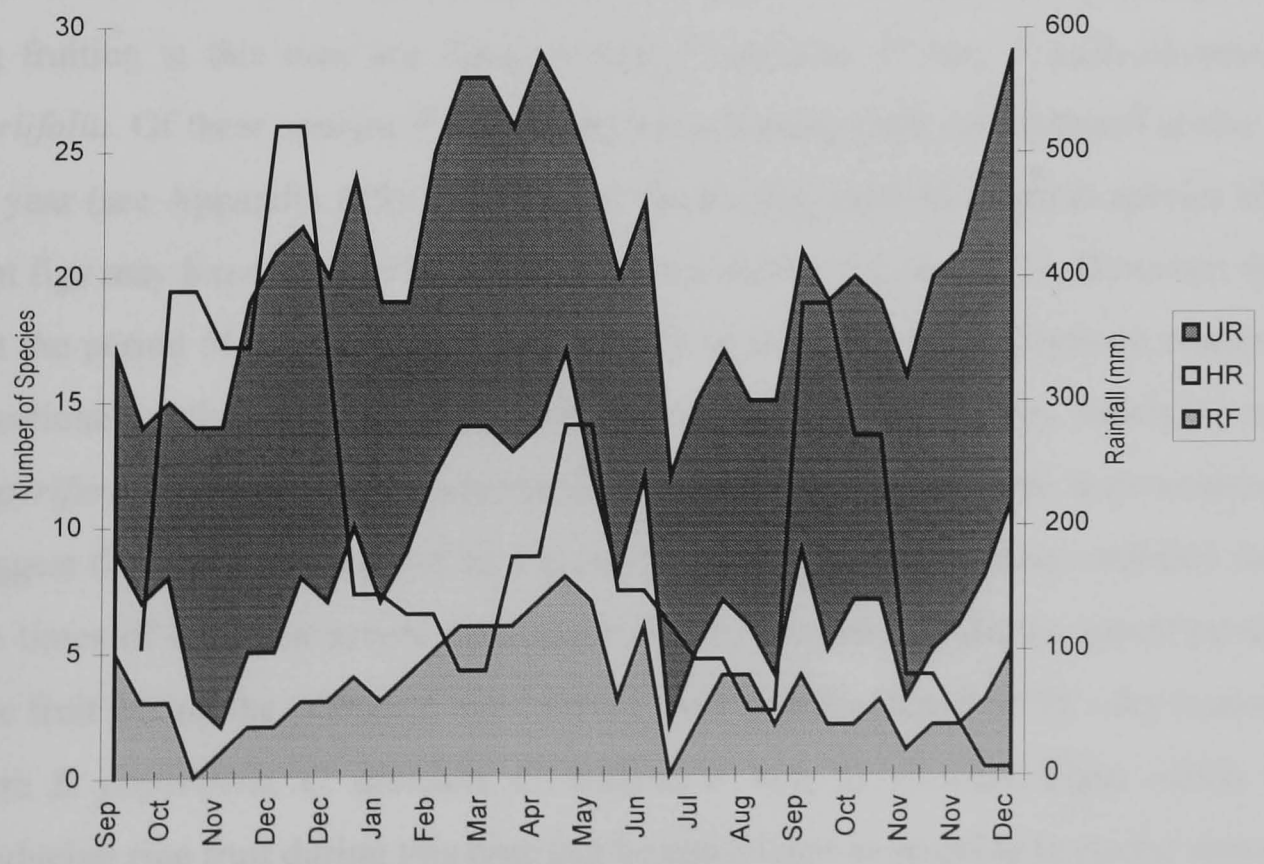


Fig 4.14 **Number Of Species** Exhibiting Each Phenology State Along The Chimpanzee Food Species Phenology Trail, Rainfall (Line).
a) **flowers (FL), buds (BD), young leaves (YL), mature leaves (ML).**



b) **unripe fruit (UR), half-ripe fruit (HR), ripe fruit (RF).**



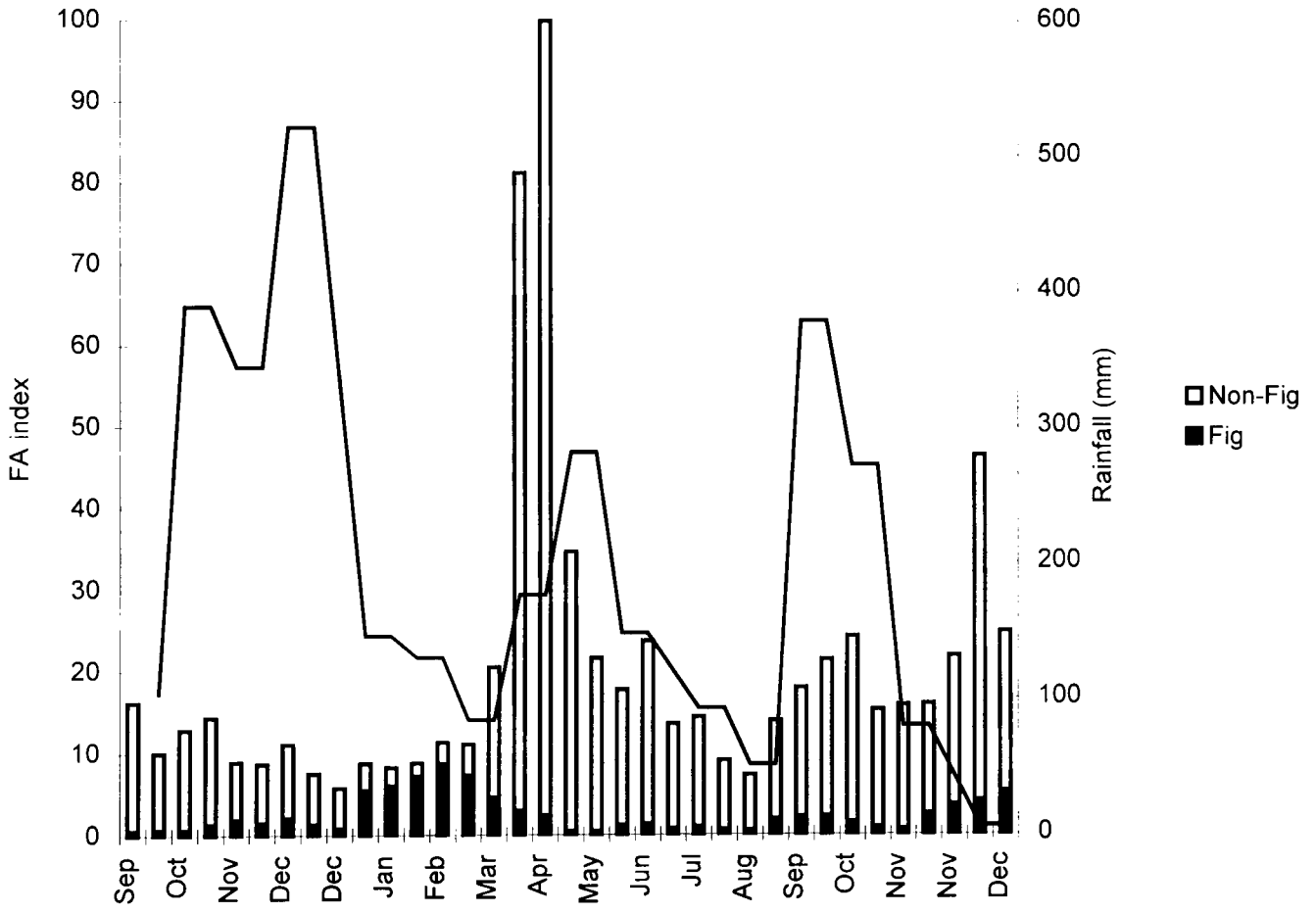
Keystone Resources.

During this study period, the time of the most severe fruit scarcity appeared to be just preceding and during the second dry season, from Jun-Aug 98 (Fig 4.9). Looking only at fruiting patterns, (Fig 4.8), the period of lowest fruit availability is also in Aug 98, coinciding with dry season(2).

In order to address the possibility of fig species acting as keystone foods, all fruiting data from the phenology trail were re-analysed without using measurements of DBH. Many *Ficus* species are stranglers, and therefore were omitted during previous analyses because their DBH could not be measured. Excluding the DBH values and including strangler figs in the analyses did not change the general patterns of fruit production. The data on fruiting patterns from the phenology trail (all fruits i.e. unripe/half-ripe/ripe) were divided into fig and non-fig species and their corresponding food availability (FA) indices calculated (Fig 4.15). Overall, the percentage of fig fruit is too small to represent on the same chart as non-fig, therefore their respective FA indices are compared. The peak in fig FA occurs during the phenology sample periods Jan - Mar 98, coinciding with a trough in the non-fig FA indices. This indicates that as a group the *Ficus* species may be an important food resource at this time. Further analyses at the species level revealed that the species of fig fruiting at this time are *F.exasperata, F. mucuso, F. sur, F.vallis-choudae, F. variifolia*. Of these species *F.exasperata* has a fruiting peak concentrated at this time of year (see Appendix B.3). Analyses of the fruiting patterns of these species shows that figs may have been an important resource during dry season(1). However, this is not the period of most extreme food scarcity so their value as a keystone resource is questioned. Other non-fig species which bear ripe fruit during dry season(1) are *B. papyrifera, C. alexandri, L. welwitschii, M. eminii, M. lactea*. There is no evidence to suggest that the *Ficus* species as a group are an important keystone resource during the times of the most severe food shortage: dry season(2). Species which produced ripe fruit during the period of most severe food scarcity, Jun-Aug 98 - dry season(2), were *B. papyrifera, C. albidum, C. milleni, F. sur, M. excelsa*. Trees which were producing ripe fruit during this time can be considered as possible keystone resources for chimpanzees. Two of these species; *B. papyrifera* and *F. sur*, were available

during both dry seasons. *B. papyrifera* and *F. sur* are the only two species in the phenology sample which produced unripe fruits in every phenological sample. However, the reproductive strategies of these two species appear to be different. *B. papyrifera* had two distinct periods of ripe fruit production coinciding with the two dry seasons. In contrast, data from the community-wide phenological sample show that ripe fruit of *F.sur* was available in every period except three periods within the months of January and June, periods of low general fruit availability.

Fig 4.15 Availability Of **Fig** Versus **Non-Fig** Fruit Along The Chimpanzee Food Species Phenology Trail (Bars), Rainfall (line).



4.6 Discussion

Methods For The Assessment Of Food Availability

A variety of methods have been used to assess fruit abundance on an individual tree for inclusion in estimates of food abundance in an area. Consequently, it may be erroneous to assume that variations in consumer species behaviour between study sites are a result of differing patterns of food availability. Although difficult to assess absolute differences in food availability between sites, standardising methods will allow accurate temporal estimations of changes in resource base within a site. This study compared results using DBH and ranks of abundance to measure food abundance. Using ranks is less time consuming and presumably less at risk of inter-observer variability, than visual counts. There are also concerns that recording abundance of phenophases does not consider that food most recently removed by the consumer, and that simply recording the tree as +/- fruit would be more appropriate (Plumptre et al., 1997). The results of this study indicate that using only DBH as a measure of food abundance correlates well with visual estimations of food abundance, however the magnitude of the peaks and troughs in food availability is lost. The degree of fluctuation between times of high food availability and scarcity may be important to primary consumers. The importance of the peaks and troughs will be greater in forests with pronounced seasonality such as Budongo, and may also be useful in inter-site comparisons of food resource base. The effect of inter-observer variability was minimised by using only one observer throughout this study. The results of the community-wide fruiting analyses showed no differences in the magnitude of the peaks and troughs, indicating that this effect may be lost when a greater number of species are included in the analyses. To conclude, the use of DBH as a measure of food abundance is less time consuming, and if a large enough sample of trees is used will give results that are equivalent to those using a visual score of abundance for each tree. Scoring individual trees for changes in food abundance will still be necessary when investigating variability between individual trees.

Another method sometimes used for estimating food availability is the number of species producing fruit. For five out of the seven phenology categories, the number of species exhibiting each phenophase was significantly correlated to the

abundance records, the exception being unripe and half-ripe fruit. In addition, although ripe fruit shows a significant correlation, there are discrepancies in the relationships between abundance and number of species and seasonality. Also, data from the community-wide correlations between abundance scores and number of species fruiting were not significant for unripe and half-ripe fruit, but they were significant for ripe fruit. Therefore, the number of species fruiting as a measure of food availability should be used with caution.

This study also investigated the correlation between the fruiting patterns of known chimpanzee food species and those of the whole forest community. The abundance patterns of ripe fruit and half-ripe fruit for chimpanzee food species were correlated with the corresponding patterns for the whole forest community, but the patterns for the number of species fruiting were not. Conversely, the number of species community-wide producing unripe fruit was correlated with that from chimpanzee food species but the abundance scores were not. These results show that it is important to include in a phenology sample as many as possible of the species in the study animal's diet. If there is no prior knowledge of the study animal's diet then a transect sample including many species would be the best approach.

Phenological Patterns of Food Availability

In general, it would appear that patterns of production are seasonal and strongly influenced by rainfall. Buds, mature leaves, young leaves, half-ripe fruit and unripe fruit were found to have significant differences in abundance when grouped into four seasons according to rainfall patterns. Interestingly, the availability of flowers and ripe fruit was not significantly related to these seasons, despite both phenophases having obvious peaks and troughs which can be explained by climatic variables. In addition, buds, young leaves, ripe fruit, half-ripe fruit were found to have seasonal differences in the number of species exhibiting each state. All phenology states except mature leaves showed an increase in production coinciding with the onset of the two rainy seasons. The other season which had a major impact on production patterns was dry season(1). Buds exhibited a peak at the beginning; flowers a peak towards the middle to end; ripe and half-ripe fruits at the end; and

mature leaves and young leaves a decrease and increase respectively. throughout dry season(1). Dry season(2) was generally associated with periods of reduced production of all phenophases, except mature leaves, and was the time of the most severe food shortage. The influence of rainfall on patterns of production is in accordance with previous studies at Budongo (Fairgrieve, 1995; Eggeling. 1947). Therefore it would appear that the unusually high rainfall at the end of 1997 did not have a major disrupting effect on the phenological patterns during this study. The availability of all phenological states is expressed as an index of 100, for each phenological state, the period with the maximum value is given the value of 100 and the food availability of all other periods shown relative to this maximum value. Therefore, it is not possible to directly compare actual quantities of food between phenological states. However, the chart of cumulative food availability illustrates the combined patterns of food availability for all the phenological states.

The peak in food production, during dry season(2), and the beginning of rainy season(2), is much reduced compared to that following the dry season(1) and the onset of rainy season(1). During this study period, there was higher rainfall during dry season(2) compared to dry season(1). This pattern is consistent across several years (see chapter 2). This indicates that it is not only rainfall which is influencing food production. The data in Chapter 2 show that levels of irradiance, measured as the number of hours of sunshine are at the annual lowest in July. Thus, it is most likely the levels of irradiance which are most strongly influencing food production during and following dry season(2). The association between peaks in irradiance and the accompanying peaks in production is well documented (van Schaik, 1993; White, 1994; Wright & van Schaik, 1994; Newbery et al., 1998). In light of these results, the patterns of production for the plant community at Budongo may be interpreted as being a balance of maximising growth during periods of maximum irradiance, whilst also being inhibited by a degree of drought sensitivity. The shedding of mature leaves during dry season(1) presumably reduces water loss via evaporation and thus protects against drought, indicating that at least some species are drought intolerant. The humidity and cloud cover during dry season(2) allow the maintenance of mature leaves. Also, young leaf production peaks at the time of maximum sunshine. then

appears to be somewhat limited during dry season(1), perhaps by water shortages and then continues with another burst of activity at the beginning of the wet season, when sunlight levels are still reasonably high and the individuals are no longer limited by drought. A strong contrast is expected between drought sensitive and drought-tolerant species when irradiance is maximal during the dry season. Leaf and flower production are predicted to occur during the wet season for drought-intolerant species and during the dry season irradiance for drought-tolerant species (Reich & Borchett, 1984; Murali & Sukumar, 1994; Barone, 1998). Presumably, species which exhibit some drought-tolerance, and thus produce buds, young leaves, flowers or fruits during dry season(1), will have a selective advantage, by maximising the benefits of long hours of sunshine for photosynthesis. Dry season leaf production may also avoid the insect herbivore abundance at the beginning of the wet season (Aide, 1992). Minimum temperature during the dry season has been found to be negatively correlated with fruit abundance in the subsequent season (Tutin & Fernandez, 1993a; Chapman et al., 1999), suggesting that it is the low temperatures rather than the low rainfall during the dry season which are influencing fruit production. It does not seem likely that minimum temperature is acting in the same way as an important cue for fruit production in Budongo Forest. If so, I would expect there to have been more fruit available in rainy season(2) i.e. the rainy season which follows directly after the coolest dry season. However, long-term phenological data investigating inter-annual variations is required to answer such questions.

During this study, all fruits, flowers, young leaves and buds were found to have a significant degree of synchrony in their patterns of production both in terms of food abundance and in terms of the number of species exhibiting each phenological state. Synchronisation of all phenological events may be a strategy adopted by plant species to minimise predation (van Schaik, 1993; Augspurger, 1996), or when the effectiveness of seed dispersal agents varies seasonally, or when large synchronous fruit displays enhance dispersal (Poulin et al., 1999). Alternatively, selection may favour temporally segregated fruiting phenologies to minimise competition and also to maintain resident populations of dispersal agents (Poulin et al., 1999, Brooke et al., 1996). The advantages of species-synchronous flowering are obvious in terms of

cross-pollination. Fruiting may occur at the same time to minimise mortality during the subsequent dry season. The time of fruiting may also be adapted to coincide with conditions favourable for germinating seedlings, which tend to be optimal early in the wet season (Garwood, 1983). It is likely that the production patterns in Budongo Forest are synchronised in order to coincide with favourable climatic variables, i.e. sunlight and rain, which are required for production of all phenophases.

Keystone Food Resources.

Chimpanzee diet is dominated by ripe fruit (see chapter 6). When considering possible keystone species, none of the species identified as fruiting during the time of the severest food scarcity was present throughout this period. This illustrates the importance of a mix of keystone species, because the importance of each species may change annually depending upon the exact climatic conditions. For example, in 1997 there was a particularly high rainfall which may have influenced the flowering and fruiting of some species. This introduces important management considerations. Of all the candidates for keystone species neither *B. papyrifera* nor *F.sur* are preferred timber species, but *M. excelsa* is a valuable timber species. Inter-annual variations in the fruiting patterns of keystone food species mean that long term monitoring is required over a variety of climatic conditions in order to make management decisions for logging. With reference to Budongo, Fairgrieve (1995) commented that dry season food shortages which are likely to occur in both logged and unlogged forest, may be less severe in logged forest due to the presence and fruiting patterns of several *Ficus* species which were not present in the unlogged forest. As a family, as species and frequently as individuals, the Moraceae exhibit phenological traits which would tend to make their new leaves or fruit available to primary consumers for much or all the annual cycle (Milton, 1991). However, in Gabon, figs are relatively rare and therefore may not be considered as a keystone food resource for most frugivores (Gautier-Hion & Michaloud, 1989). Newton-Fisher (1999b) stated that at Budongo figs should be considered a staple rather than a fallback food. Certainly, the almost constant availability of *F. sur* means that it could be used as a staple. In

addition, all Ficus species may be considered as important resources during dry season(1).

The effects of spatial and temporal differences in phenology patterns have been demonstrated in long term studies (Chapman et al., 1999; Tutin & White, 1998). At Kibale Forest, Uganda, which has a similar bi-modal rainfall pattern to Budongo Forest, two sites were sampled for phenological information. One site, Kanyawara, exhibited regular annual peaks in flowering and fruiting patterns. At the other site, Ngogo, there were no regular fruiting patterns and flowering peaked immediately after the maximum period of irradiance. At Kanyawara, fruiting patterns were found to peak at the end of the first wet season and at the beginning of the second dry season. In addition, some species trends which were suggested from one year of data were not supported when additional years were added. Phenology patterns at Lopé, Gabon, have also shown that some species have irregular inter-annual variations in the size and/or timing of ripe fruit crops (Tutin & White, 1998). For these reasons the results of this study should be considered preliminary and only relevant to the area of forest studied.

4.7 Conclusions:

- There is marked seasonal variation in the availability of chimpanzee food species.
- There is synchrony between phenological states
- The availability of food is closely linked to irradiance levels and drought sensitivity
- There are distinct climatic differences between dry season(1) and(2) resulting in Budongo Forest being best described as experiencing four seasons.
- The availability of chimpanzee food was generally correlated with that of the whole forest community.
- Several keystone species were identified and the importance of a mix of species was stressed.

Chapter 5

Grouping Patterns

5.1 Introduction

Understanding the adaptive significance of grouping patterns is central to the study of primate behavioural ecology. Many benefits and costs associated with group living have been proposed. Generally, the most important selective advantages of living in a group are increased protection from predators, increased likelihood of finding or defending food resources, and protection against harassment or infanticide. To be weighted against these benefits are the costs of group living such as increased competition for food, increased conspicuousness to predators, increased disease transmission and harassment from other group members. Individuals are expected to behave in an optimal manner, i.e. minimising the costs and maximising the benefits associated with group living. There have been many comparative studies which support these arguments (Pulliam & Caraco, 1984; Krebs & Davies, 1993).

The Social Structure of Chimpanzees

All studies of chimpanzees populations, both *P. troglodytes* and *P. paniscus*, have described a fission-fusion social system (Goodall, 1986; White, 1988). These fluid societies are believed to exist in species free from predation (but see Boesch, 1991) as a flexible strategy to minimise feeding competition. Two types of feeding competition can be distinguished 1) *scramble competition* and 2) *contest competition*. Scramble competition occurs where individuals share a food resource and no individual is able to exclude another from access to the resource. The net food intake of all individuals in a population is almost equally affected by an increase in the population density (van Schaik, 1989). Contest competition occurs whenever the distribution of food will allow overt contest for food leading to differential intake of food for different individuals in the same population. Most individuals will experience a combination of both types of competition. There are two situations

within which both contest and scramble competition may occur: 1) within a group; 2) between groups. This results in four competitive regimes 1) competition mainly by within-group scramble competition; 2) competition by within-group contest competition and a variable intensity of within-group scramble competition; 3) competition mainly by within-group scramble competition and between-group contest competition: 4) competition mainly by between-group contest competition, usually with an unexpressed potential for strong within-group contest competition (van Schaik, 1989). Chapter 1 discussed how the effects of these competitive regimes should be expressed in the social relationships of females (Wrangham, 1980; van Schaik, 1989; Sterck, 1997).

All studies of the diet of chimpanzees have found fruit to be the major component. The distribution of fruiting trees is usually in discrete clumps or food patches. As a rule, high quality foods such as fruits are more dispersed than lower quality foods such as leaves. However, even folivores may be selective about which leaves they choose from the seemingly ubiquitous distribution in tropical forest (Strier, 2000). The group size in frugivorous primates may be predicted by the cost of additional travel imposed by extra companions (Janson & Goldsmith, 1995). The greater the 'cost' of having an additional group member in terms of travel, the smaller the group. In addition, frugivorous primates may adjust the size of feeding party to the size of the feeding patch (Leighton & Leighton, 1982; Symington, 1988; Strier, 1989; de Moraes et al., 1998). Dunbar (1988) emphasises that it is not only the size of food patches which is important in determining grouping patterns but also the distances between these patches, Thus, for frugivorous primates there are two primary factors influencing feeding competition and the resultant grouping patterns: the size of feeding patches and the distances between these feeding patches.

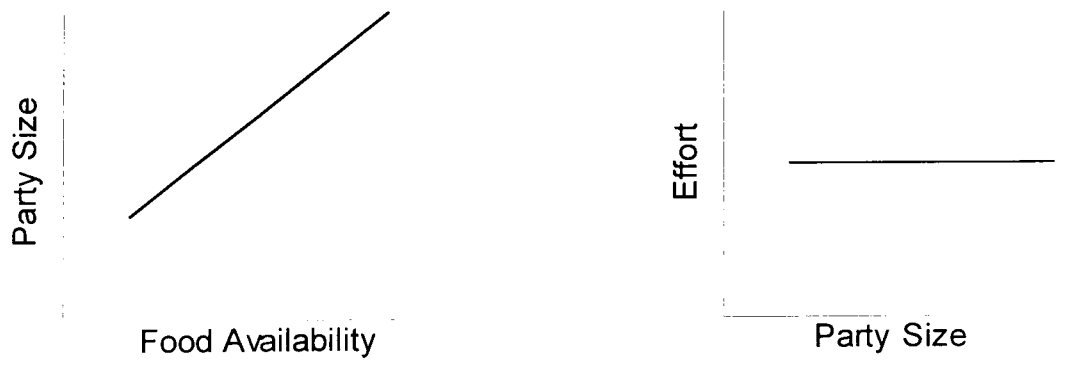
The relative importance of the various factors influencing group size are difficult to assess in species living in stable groups. However, the fluid society of species characterised by fission-fusion grouping patterns offers an unique opportunity to study these factors. Fluctuations in the size of the temporary parties in fission-fusion societies should reflect the fluctuating benefits and costs associated with group living. Van Schaik (1999) suggests that two kinds of fission-fusion

organisations exist; those that exist usually as a stable group which may occasionally fission into smaller groups for feeding, but can be regularly found as a complete social unit (group-based fission-fusion); and individual-based fission-fusion. for example chimpanzees and orangutans, whose social unit may only be determined by examination of association patterns.

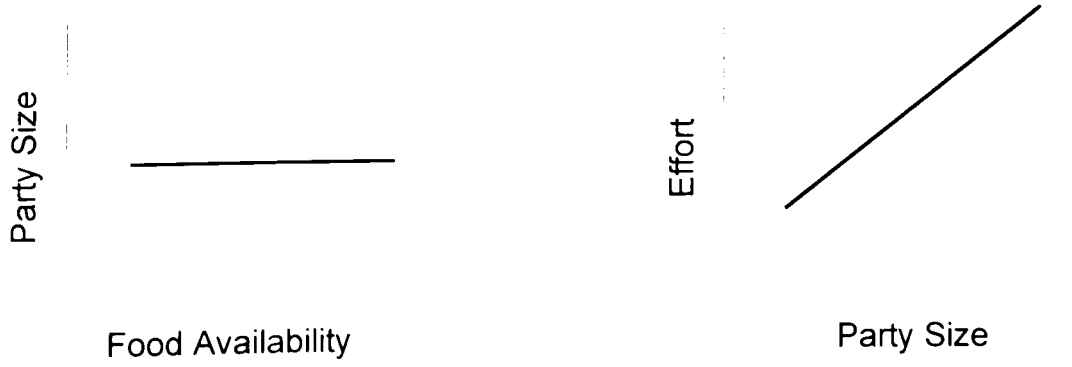
The benefits of grouping in chimpanzees, and indeed in any fission-fusion society, may in addition to the already highlighted benefits, include social benefits which are normally available all the time to species living in stable groups, for example protection of offspring, mating opportunities, assessment of possible mating partners etc. Van Schaik (1999) suggests two models of the benefits of grouping a) when the benefits of grouping are always available, b) when the benefits of grouping are sporadic. When the benefits to grouping are always available then party size is expected to be positively related to food availability, however if the benefits are sporadic and unrelated to food availability then there will be no correlation of party size with food availability.

Fig 5.1 The Expected Relationship Between Food Abundance And Party Size And Travel Effort [from van Schaik (1999)].

a) when the social benefits of association are always available and can thus be obtained opportunistically.



b) when benefits arise sporadically (and independently of food availability), animals obtain them whenever possible.



Many factors, both ecological and social, have been proposed to be important in determining party size in chimpanzee communities. The importance of food density and distribution has been emphasised by many. (Ghiglieri, 1984; Isabyre-Basuta, 1988; Wrangham, 1986; White & Wrangham, 1988; White, 1992; Wrangham et al., 1992; Chapman et al., 1994a, 1995; Wrangham et al., 1996; Doran, 1997). Goodall (1986) suggested sex as the most important determining factor, as large parties contained sexually receptive females. Boesch (1991) highlighted the importance of predation pressure. Sakura (1994) and Boesch (1996) illustrate the importance of community demography in determining fission-fusion patterns. Some studies have identified more than one factor influencing grouping patterns. The grouping patterns of the savanna-dwelling chimpanzees in Senegal were thought to be more heavily influenced by the threat of predators and the availability of water and nesting sites than the availability of food (Tutin et al., 1983). Boesch (1996) concludes that the number of oestrous females, general food availability and hunting rate all influence the size of sub-group. Further research from Gombe found that perceived low food availability during the dry season, increased the number of females in oestrus and high hunting rate coincided to produce larger parties (Stanford et al., 1994); and at Mahale, Matsumoto-Oda (1998a) found that both food availability and the presence of oestrous females independently affected grouping patterns. Boesch & Boesch-Achermann (2000) state that community size and sex ratio are important factors in determining the observed differences in party size and type between populations, illustrating that smaller communities are more cohesive

A core party structure, in which all or most of the community's adult males are present, has been observed (at least seasonally) at Mahale, Gombe, Bossou and Tai (Boesch & Boesch, 1989) and for bonobos at Wamba (Furuichi, 1989). At Bossou, all members were observed in the same sub-group in 18.8% of all observations; even after the decrease in adult males to only a single male, the group maintained cohesion (Sugiyama & Koman, 1979; Sugiyama, 1981; Sugiyama, 1988). At Budongo during a recent study, no core parties were observed (Newton-Fisher, 1997). This may in part have been due to the turbulent male hierarchy at the time, as the alpha male was defeated (Newton Fisher, pers. comm.). During the present study,

core parties were seen. The occurrence of a core party structure suggests that there are at least temporary benefits to grouping.

Comparison of P. troglodytes *and* P. paniscus *Social Organisation.*

Inter-site and inter-species comparisons of behavioural ecology have been made to try and identify the factors determining social organisation (*P. paniscus* vs. *P. troglodytes*; Wrangham et al., 1996; Chapman et al., 1994; Chapman et al., 1995; Wrangham, 1986; Malenky et al., 1994; *P. troglodytes* vs. *Ateles* spp. Symington, 1990). Both species of chimpanzee, common and bonobo, are highly frugivorous and both display a fission-fusion social organisation in which individuals are found in parties that are flexible in size. However, there are some major differences in social structure (White, 1996; Stanford, 1998). Bonobo females exhibit high levels of affiliative behaviour, parties are based on cores of females that regularly associate, and maintenance of feeding proximity also reflects strong social bonding among females (White & Lanjouw, 1992). Bonobo females exhibit longer periods of sexual swellings. Males show little affiliative behaviour and all-male parties are absent. Inter-community relations are very different. Bonobos have been observed to interact peacefully at inter-community encounters, whereas chimpanzee males are known to stalk out members of adjoining communities with an intent to kill (Goodall, 1986; Wrangham, 1999). These behavioural differences are thought to be the result of differential ecological costs of grouping, i.e. female relationships in the common chimpanzee are thought to be constrained by feeding competition leading to the formation of smaller sub-groups.

Three ecological hypotheses have been proposed to explain these differences in social structure. First, it was suggested that variation in food patch size in different forest habitats was important, the patch size being larger for bonobos, thus accommodating more individuals and allowing the formation of alliances (White & Wrangham, 1988). However, study of tree measurements found the size and density of fruit trees used by the two species at Kibale and Lomako to be essentially similar (Chapman et al., 1994a). Chapman et al. (1994a) suggest that it may be the temporal difference in availability of resources which is important in shaping social structure

i.e. chimpanzee habitats may have periods of high abundance alternating with periods of scarcity, while at the bonobo site the food availability may remain relatively constant. Availability and use of terrestrial herbaceous vegetation, (THV), in the different habitat types was also considered important (Malenky & Wrangham, 1994; Malenky et al., 1994). Wrangham et al. (1996) observed that chimpanzees use THV as a back-up food in periods of fruit scarcity whereas bonobos use THV all year round. It is suggested that the quality of THV available to bonobos is higher than that available to chimpanzees. Malenky (1990) suggested that the seasonal variance in food production may be less for bonobos, but seasonality in lowland forests is strongly related to latitude (van Schaik et al., 1993) so fruiting seasonality is unlikely to differ consistently between the two species which, although not sympatric, do occur at similar latitudes. Recently, Wrangham et. al. (1996) have suggested that it may be better to look at comparative locomotion costs to explain the difference in social organisation. As more data become available, it can be seen that there is substantial variability in mean party and community sizes of bonobos and chimpanzees (see Table 5.1). Therefore, detailed studies of the ecological correlates of grouping patterns in each species of chimpanzees in differing habitats will identify the range of variation both within and between the two species, and thus help in understanding the factors influencing the two social organisations. Forests are assumed to have less seasonal variation in food availability than the savanna woodland and gallery forest of Mahale and Gombe. However, detailed results from two forested *P. troglodytes* sites, Kibale and Tai, show that food availability is of differing importance to the grouping and association patterns of the chimpanzees (Wrangham et al., 1996; Doran, 1997; Boesch & Boesch-Achermann, 2000). Of all the studies of grouping patterns in *P. troglodytes* to date only those at Kibale (Wrangham et al., 1992) have reliable phenology data to assess the effect of temporal variation in fruit availability on grouping patterns.

Many questions remain to be answered concerning the factors affecting grouping patterns. Are selection pressures reflected by how primates behave most of the time, or how they behave during critical times when their survival is at stake? (Strier, 2000). Additionally, the compromises between selection pressures associated

with food distribution, predator avoidance and social variables are difficult to distinguish. Comparisons of the same species in different locations in both time and space are necessary to draw conclusions on the variability and adaptability of species.

Table 5.1 Mean Party Size And Community Size For Different Populations Of Chimpanzees.

Population	Mean Party Size	Community Size
Chimpanzees		
Bossou	4	20
Budongo	5.7	46
Gombe	4	64
Kibale	5.1	27
Mahale	6.2	29
Tai	10.0	76
Bonobos		
Lomako	5.4	
Blobs	4.3	10
Hedons	7.1	22
Rangers	9.7	21
Wamba		
Kuroda	16.9	58

Bossou: Sakura (1994); Budongo: Newton-Fisher, (1997); Gombe: Goodall (1968); Kibale: Chapman et al. (1994); Mahale: Nishida (1968); Tai: Boesch & Boesch-Achermann (2000); Lomako: White (1988, 1989, 1992); Wamba: Kuroda (1979).

5.2 Aims

This study will investigate the influence on party size of the ecological factor of variation in food availability and the social factor of variation in the availability of females in oestrus. The following hypotheses will be tested:

Hypothesis 1: There are constant benefits to being in a large group. In which case a positive correlation between party size and measures of food availability would be expected.

Hypothesis 2: One benefit of grouping may be the presence of oestrous females in the community. The hypothesis that party size increases when there are oestrous females in the community will be tested.

Hypothesis 3: Different age-sex classes may differ in their sociability due to variation in the nature and strength of benefits and costs. The grouping patterns of different age-sex classes will be determined.

Hypothesis 4: The relationship between the two factors presumed to be affecting grouping patterns, food availability and the number of females in oestrus will be investigated.

5.3 Methodology

Party Size And Composition

Comparisons of grouping patterns between sites are often complicated by differences in methodology as well as site differences in habituation levels, predation pressures etc. The definition of what constitutes a sub-group or party varies between observers and study sites. Methods used include:

- recording all individuals within 100m of the target animal (Wrangham & Smuts, 1980; Goodall, 1986)
- recording all individuals within 50m, (although it is noted that in practice it is difficult to measure precise distances, therefore parties are discrete units separated by unknown distances (Wrangham et al., 1992).
- recording all individuals within sight of the observer recorded continuously (Boesch, 1996; White, 1989).
- recording all individuals seen on one day, whilst following one group (Matsumoto-Oda et al.,1998).

In addition authors differ in their definitions of which individuals are party members, and have sometimes included all individuals, or only adults and adolescents, or all independent individuals. Chapman et al. (1993) highlight the difficulties in defining sub-group size. Habitat visibility, habituation levels and method of location will all affect the recorded party size. Locating chimpanzees by vocalisations in two communities in Kibale forest resulted in subgroups which were twice as large as those found by checking fruit trees. Chapman et al. (1993) recommend that studies

should include a good description of habitat visibility, the degree of habituation and how the sub-groups were located. They also suggest that in instances where individual recognition is possible, sub-group size may be recorded during successive scans made over a long period of time, such as all individuals seen within one hour. This method would be less likely to omit animals from the sub-group that were present all along but were temporarily out of the observers' view, thus decreasing the significance of level of habituation and visibility conditions.

In Tai, comparison of a continuous recording technique versus one based on 1 hour interval sampling on the same days, with the same target individual, produced significantly divergent results for both party size and party type. The second method underestimated small party sizes and over-estimated the size of mixed parties. Smaller parties have shorter duration than larger ones, so excluding the duration over-estimates the importance of small parties (Boesch & Boesch-Achermann, 2000).

In order to minimise the effects of differing methodologies when comparing results between studies, the same methodologies were used in this study as by Newton-Fisher (1997) in a previous study of this community. The total number of independent individuals in a party was recorded every 15 min (total number of scans = 5296). For the analyses, only scans which included a change in party membership were included i.e. a community member had either joined or left the party (3095 scans). This method allows the behaviour of the chimpanzees to determine the definition of separate parties. Each act of joining or leaving a party is interpreted as a 'decision' to stay or leave a party. This will reduce problems of statistical dependency between parties. However, the duration of parties with a particular group size will be lost (see Boesch 1996; Boesch & Boesch-Achermann, 2000). From this sample of independent parties; the mean party size for each two week phenology period was calculated (n=32). As the phenology data were only available from September 1997 onwards, the number of scans used in these comparisons was 2756. There were no data on party size available for the periods December 1997, and December 1998. These mean values were then correlated with the phenological variables, (fruit and leaves), described in chapter 4.

In order to investigate the effect of oestrous females on the grouping patterns, the number of oestrous females (individuals exhibiting a sexual swelling scored as 3 or 4) observed in each two week period were counted.

In order to look at the effects of variation of food availability and number of oestrous females on different types of parties, all parties were divided into four types (see Table 5.2).

Table 5.2 Party Types (modified from Goodall, 1986).

Party Type	Description
Sexual	mixed party in which one or more of the females is in oestrous.
Mixed	one or more adult or adolescent males with one or more adult or adolescent females.
All Male	two or more adult/adolescent males.
All Female	two or more adult/adolescent females inc. oestrous and non- oestrous states.

5.4 Analyses

The Mann-Whitney test was used to examine differences in the size of different party types. Pearsons correlation coefficient was used to correlate the various measures of food availability and the number of oestrous females with party size. In order to perform this parametric statistical analyses, the following variables were $\log_{10}$ transformed in order to normalise the data: all the variables from the phenology trail of chimpanzee food species; the mean party size data for sexual and all-female parties. I used a General Linear Model to test the independent effects of food availability and number of oestrous females on party size.

5.5 Results

Analyses of Party Size and Type.

Fig. 5.2 Frequency Of Different Party Sizes For All Party Types, June 1997- December 1998, (N= 3097).

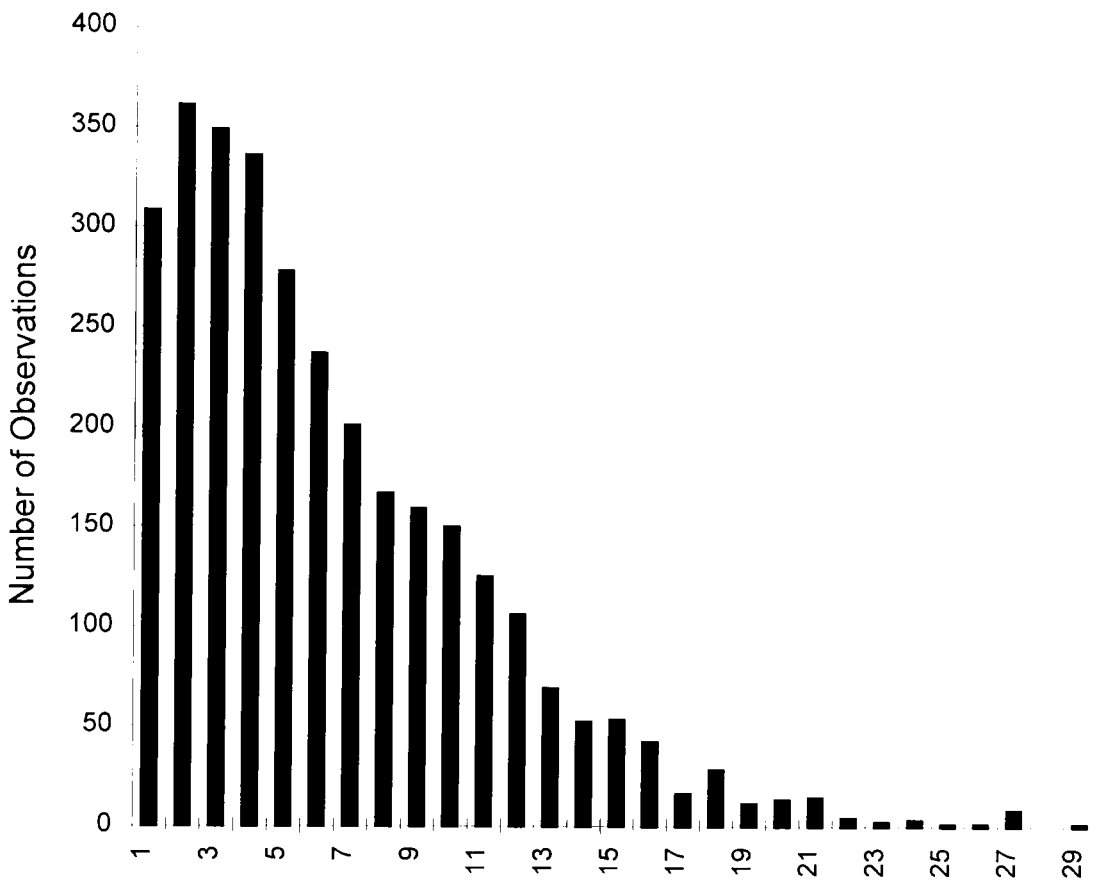


Table 5.3 Mean Party Size For Each Party Type

Group Type	N	Mean	Median	Max	St Dev.
All parties	2756	6.36	5	29	4.62
Sexual	1030	9.56	9	29	4.87
no of females	1030	3.45	3	15	2.66
no of males	1030	5.93	5	15	3.36
Mixed	831	5.98	5	20	3.27
no of females	831	3.02	3	14	2.20
no of males	831	3.17	2	16	2.33
All Female	463	2.30	2	8	1.43
All Male	311	2.54	2	8	1.55
?	121	7.09	7	13	2.70

(?, when the oestrous state of females was not recorded)

Table 5.4 Percentage Of Different Party Types.

Party Type	Percentage of Parties
Sexual	37.4
Mixed	30.2
All Female	16.8
• *Females Alone*	*(36.9)*
All Male	11.3
• *Males Alone*	*(31.5)*

During this period of data collection there were 19 independent females and 18 independent males in the Sonso community, including Chris,CH, who disappeared during September 1997, Kikunku, KK, who disappeared during June 1998 and Zesta, ZT, who died in November 1998. The mean party size for all party types combined was 6.36 +/- 4.6 (Fig 5.2; Table 5.3), lone individuals were included in the calculation of mean party size. The size of sexual parties was significantly larger than that of mixed parties (Mann-Whitney U: n1= 1030; n2= 831, U= 229414.5, z= -17.282, $p<0.001$). The size of all-male parties was significantly larger than that of all-female parties. (Mann-Whitney U: n1= 463; n2= 311, U= 65480.0, z= -2.216, $p<0.05$). The size of mixed parties was significantly larger than that of all-male parties. (Mann Whitney U: n1= 680; n2= 281.6, U= 39060.5, z= -18.294, $p< 0.001$). There were significantly more males in sexual parties than females (Mann Whitney U: n1, n2 = 32, U= 505.5, z= -2.095, $p<0.001$). There were no significant differences in the mean number of females and males in mixed parties (Mann Whitney U: n1, n2= 32, U= 991.5, z =-0.1350, ns.). The most frequent party type was bisexual, either mixed party or sexual party (Table 5.4). There were similar proportions of all-female and all-male parties; and solitary female and solitary male parties (Table 5.4).

One-way ANOVA analyses were used to investigate variation between mean party size for each two week period for each party type over the duration of the study. Each party type showed significant variation in mean party size between two week periods. (Mixed parties $F_{31, 799}= 3.42$, $p<0.001$; Sexual Parties $F_{27, 1002}= 9.92$, $p<0.001$; All-male parties $F_{31, 431}= 1.99$, $p<0.01$; All-female parties $F_{31, 431}= 5.22$, $p<0.001$, see Figs 5.3; 5.4). There was also considerable variation in the frequency of parties observed between two week periods (Fig 5.5).

Fig 5.3 Temporal Variation In The Mean Size Of All-Female, All-Male Party Types and All Group Types Combined.

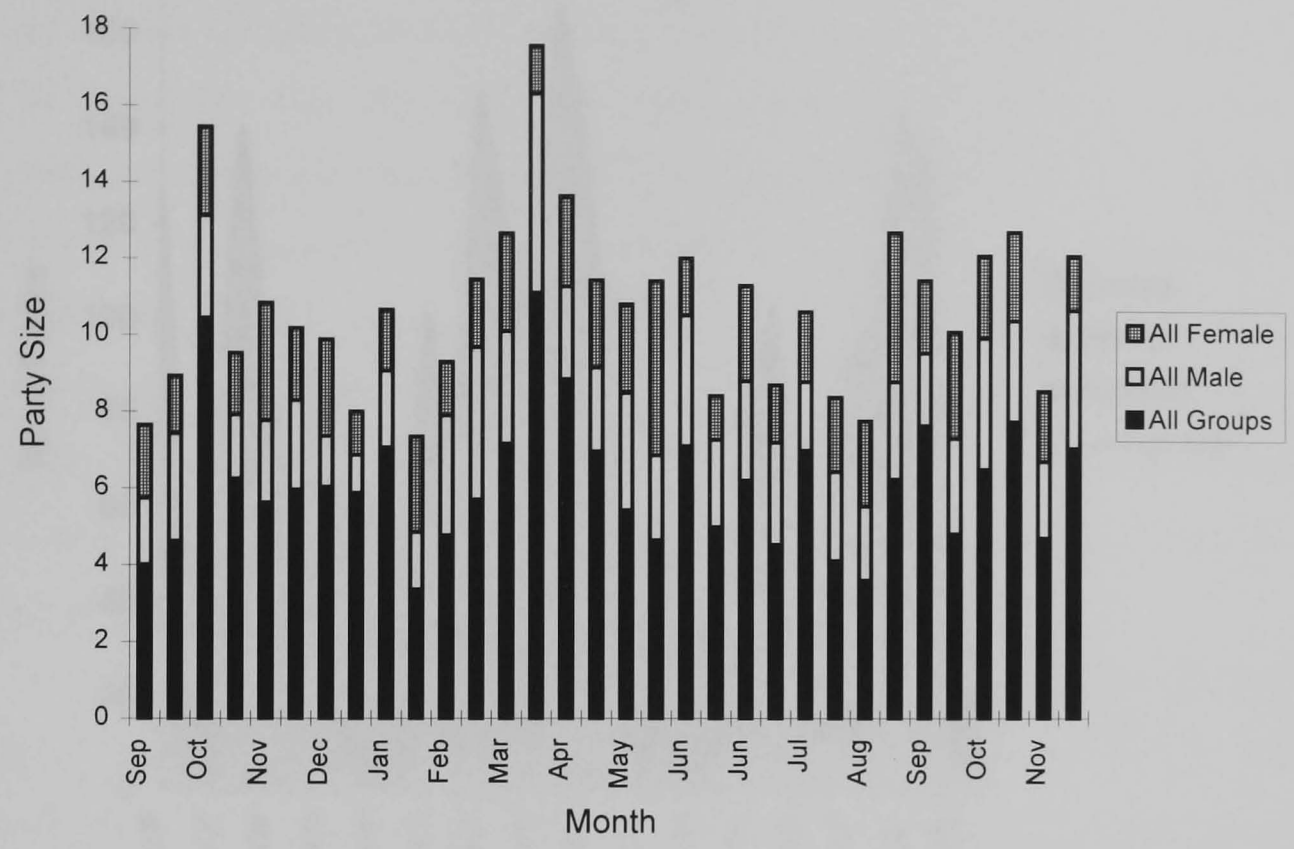


Fig 5.4 Temporal Variation In The Mean Size of Sexual and Mixed Party types.

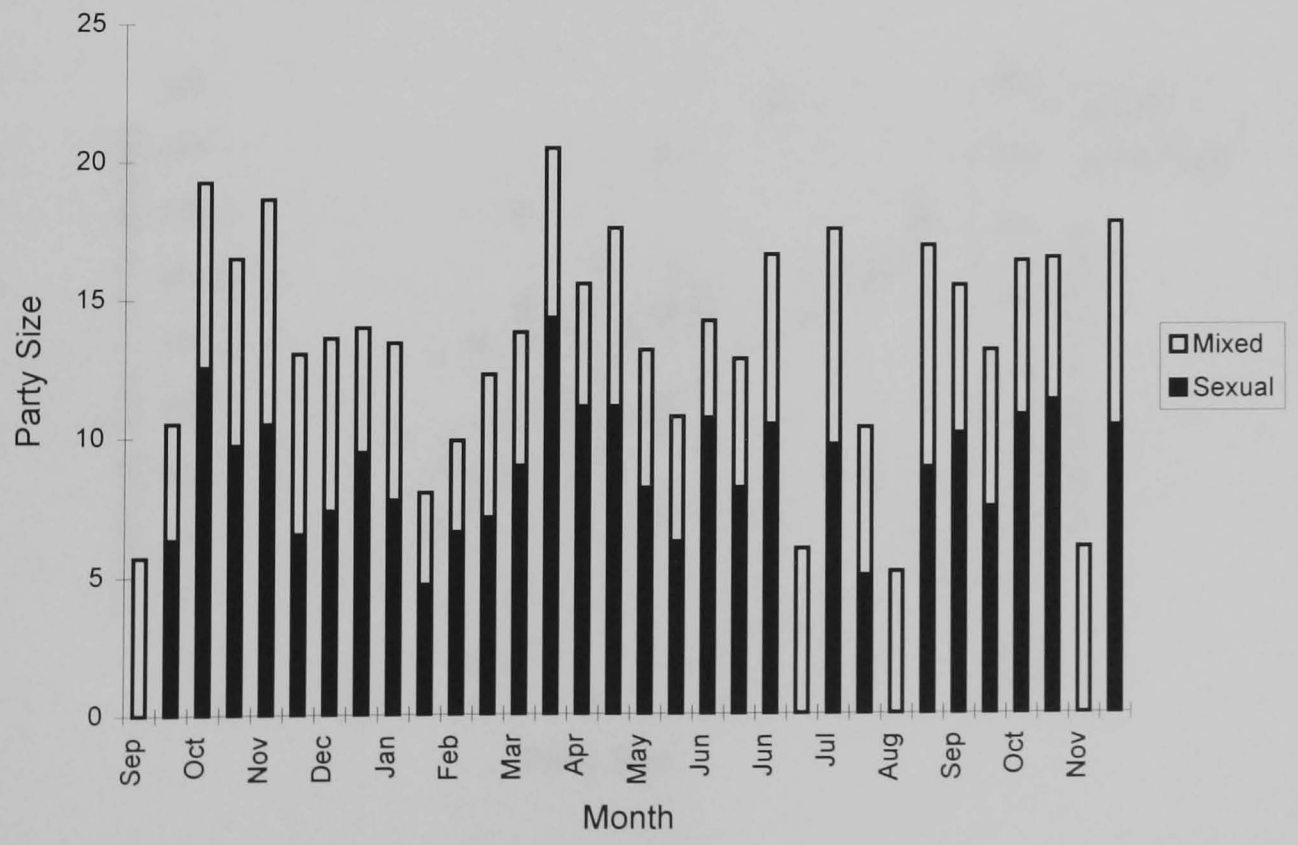


Fig 5.5 The Frequency Of Different Party Types; Sexual, Mixed, All-Male, All-Female, Observed In Each Two Week Period

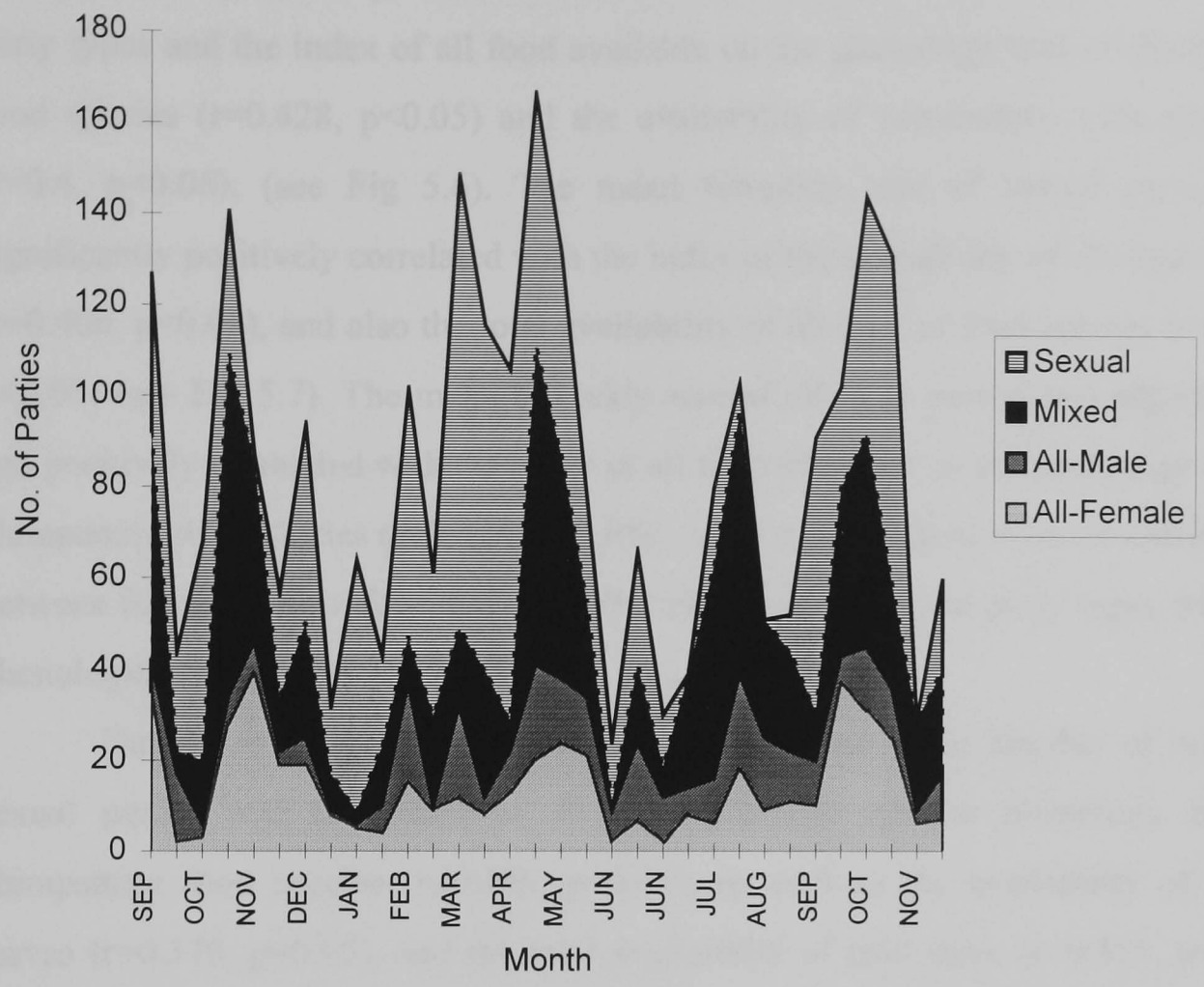
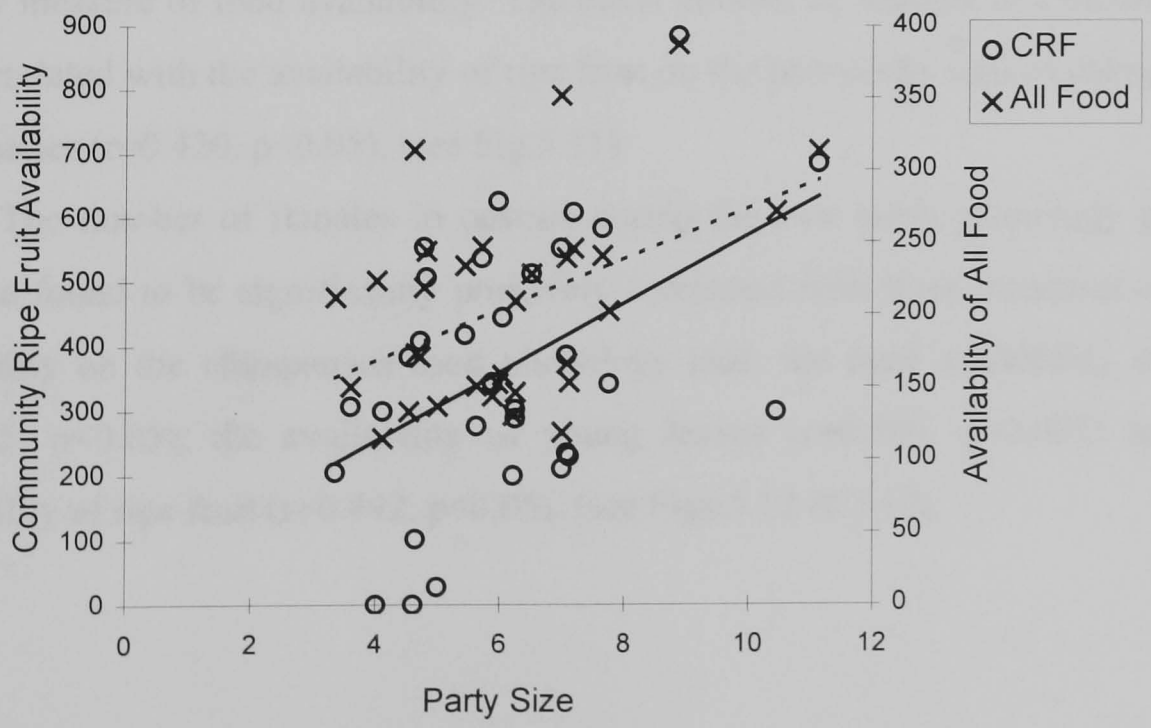


Fig 5.6 The Relationship Between Party Size (all party types) and Food Availability. [CRF = community-wide availability of ripe fruit (solid line), all food = the availability of all food types along the phenology trail (dashed line)].



Correlations of Party Size and Phenological Variables.

There was a significant positive correlation between the biweekly mean size of all party types and the index of all food available on the phenology trail of chimpanzee food species ($r=0.428$, $p<0.05$) and the availability of community wide ripe fruit ($r=0.4$, $p<0.05$), (see Fig 5.6). The mean biweekly size of sexual parties was significantly positively correlated with the index of the availability of all food species ($r=0.406$, $p<0.05$), and also the total availability of all fruit of food species ($r=0.440$, $p<0.05$) (see Fig 5.7). The mean biweekly size of all-male parties was significantly and positively correlated with the index of all food available on the phenology trail of chimpanzee food species ($r=0.424$, $p<0.05$), (see Fig 5.8). There were no correlations between the mean biweekly size of all-female parties or mixed party types with any phenological variables.

There was a significant correlation between the mean number of males in sexual parties and the index of all food available on the phenology trail of chimpanzee food species ($r=0.396$, $p<0.05$), as well as the availability of young leaves ($r=0.370$, $p<0.05$), and the total availability of fruit there ($r=0.351$, $p<0.05$), (see Fig 5.9). The mean number of females in sexual parties was significantly correlated to the availability of young leaves ($r=0.453$, $p<0.01$) (see Fig 5.10). There were no significant correlations between the mean number of males in mixed parties and any measure of food availability. The mean number of females in a mixed party was correlated with the availability of ripe fruit on the phenology trail of chimpanzee food species ($r=0.420$, $p<0.05$), (see Fig 5.11).

The number of females in oestrus during the two week phenology periods was also found to be significantly positively correlated with three measures of food availability on the chimpanzee food phenology trail; the total availability of food ($r=0.425$, $p<0.05$); the availability of young leaves ($r=0.586$, $p=0.001$) and the availability of ripe fruit ($r=0.442$, $p<0.05$), (see Figs 5.12 & 5.13).

Fig 5.7 Relationship Between **Sexual** Party Size and The Availability of All Food Items Combined (dashed line) and All Food (solid line) Availability Along Phenology Trail.

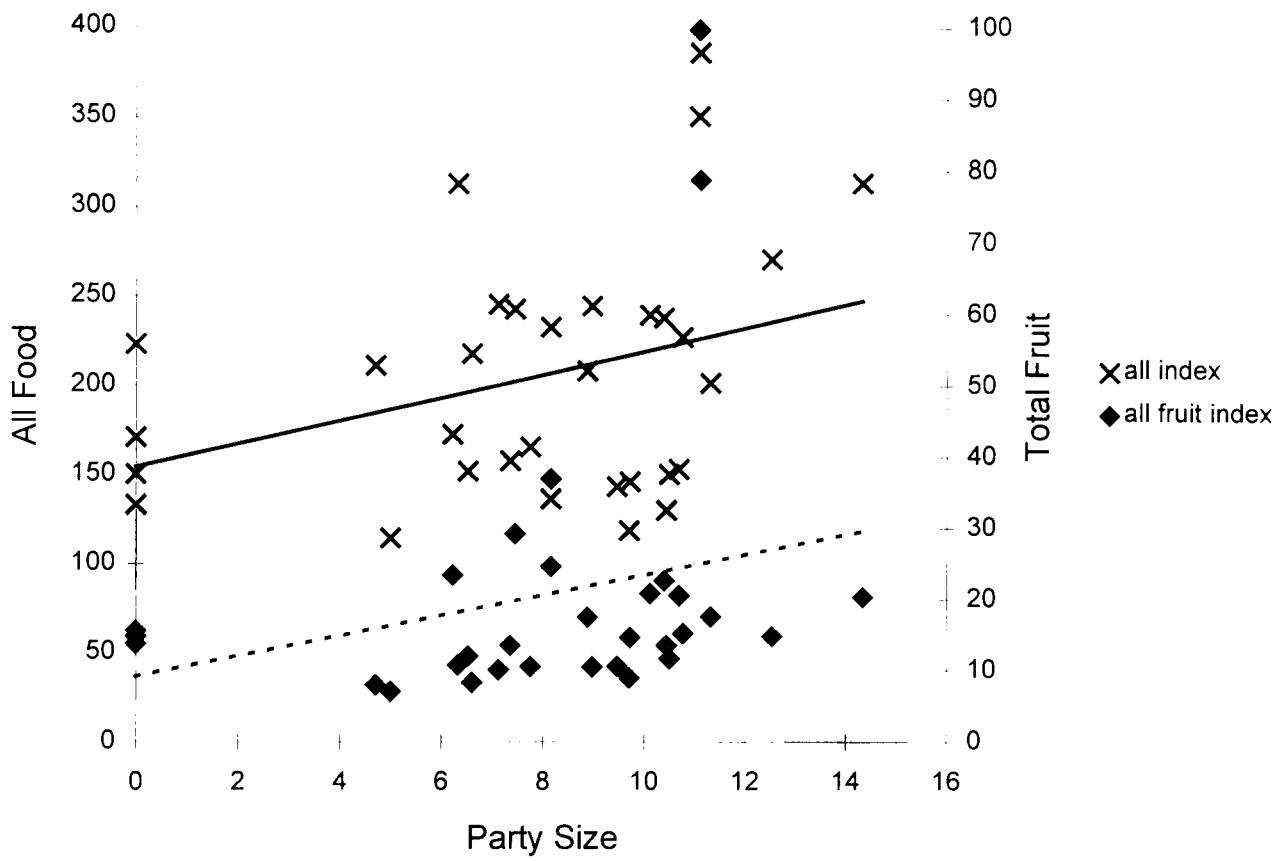


Fig 5.8 Relationship Between **All-Male** Party Size and the Availabilty of All Food Items Along the Phenology Trail.

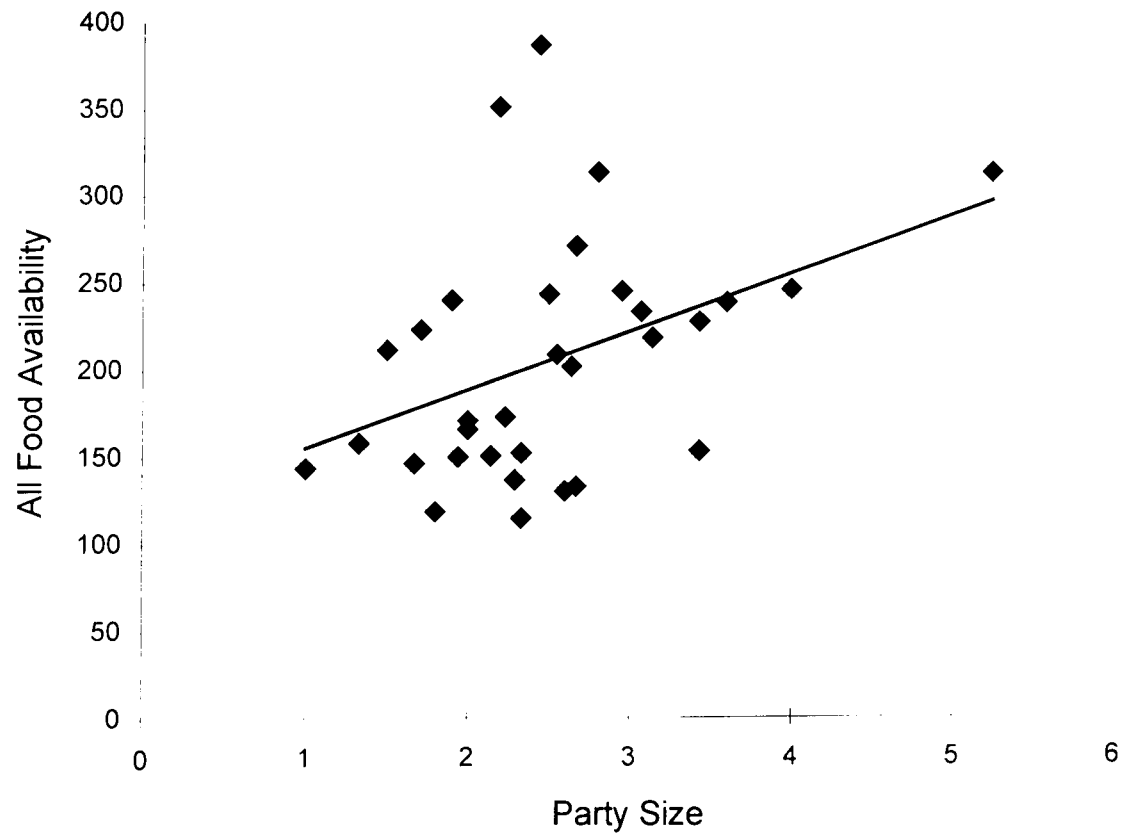


Fig 5.9 The Relationship Between **The Mean Number of Males in Sexual Parties** and Measures of Food Availability, [AF=all food (dotted line), AFR = All Fruit (dashed line), YL = young leaves(solid line)].

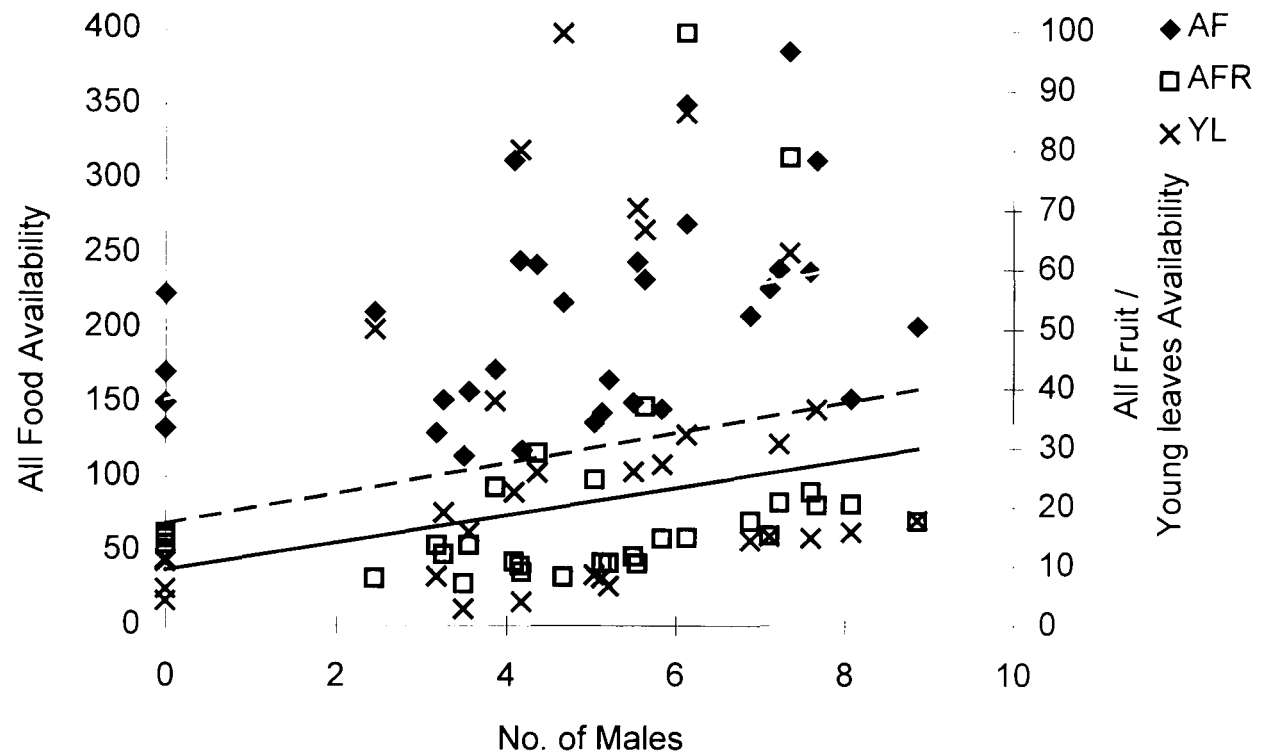


Fig 5.10 Relationship Between **The Number of Females in Sexual Parties** and the Availability of Young Leaves.

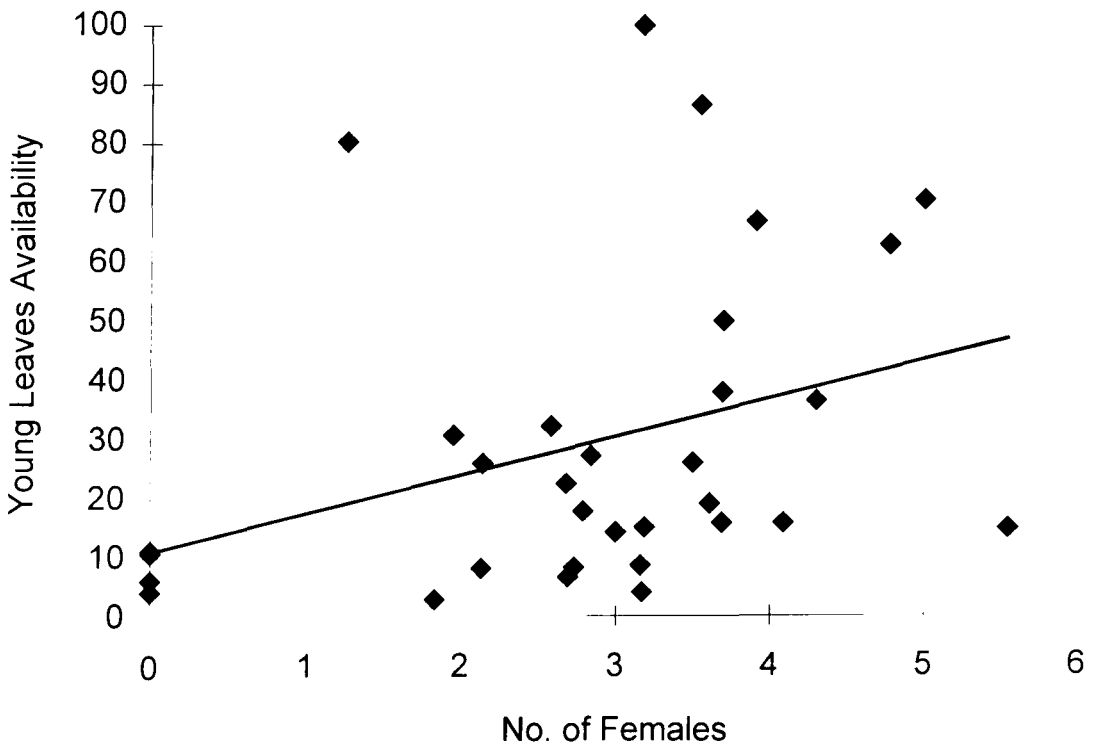
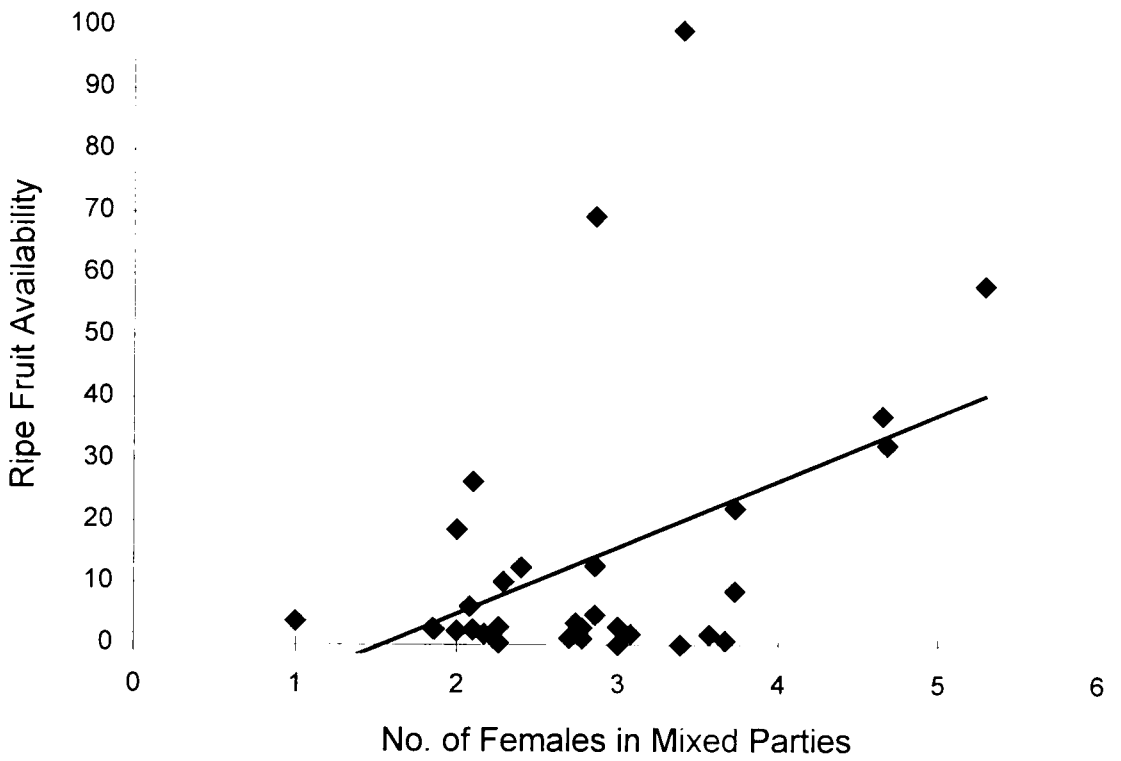


Fig 5.11 The Relationship Between **Mean Number of Females in Mixed Parties** and the Availability of Ripe Fruit.



Relationship Between Party Size and Availability of Oestrous Females.

The majority of sexual parties contained one oestrous female (Fig 5.14). The size of the sexual party was correlated with the number of oestrous females in a party (Fig 5.15), however above three oestrous females there appears to be no further increase in party size. Party size may then be limited by the size of the food patch or by simply the number of community members.

When considering all group types together there was no significant correlation between party size and the number of females in oestrus during each two week period. However, there are significant positive correlations between the number of oestrous females and party size of sexual and all-male party types (sexual $r=0.477$, $p<0.01$; all-male $r=0.370$, $p<0.05$, Fig 5.16). There was a significant negative relationship between the number of oestrous females and the size of mixed parties ($r=-0.470$, $p=0.05$, Fig 5.16). There was no correlation between the number of oestrous females and the size of all-female parties. The mean number of females or males in sexual or mixed party types is not significantly correlated with the number of oestrous females.

Fig 5.12 Temporal Variation In The Number of Oestrous Females Available In the Community (Bars) And The Availability of All Food Items Along The Phenology Trail (Line).

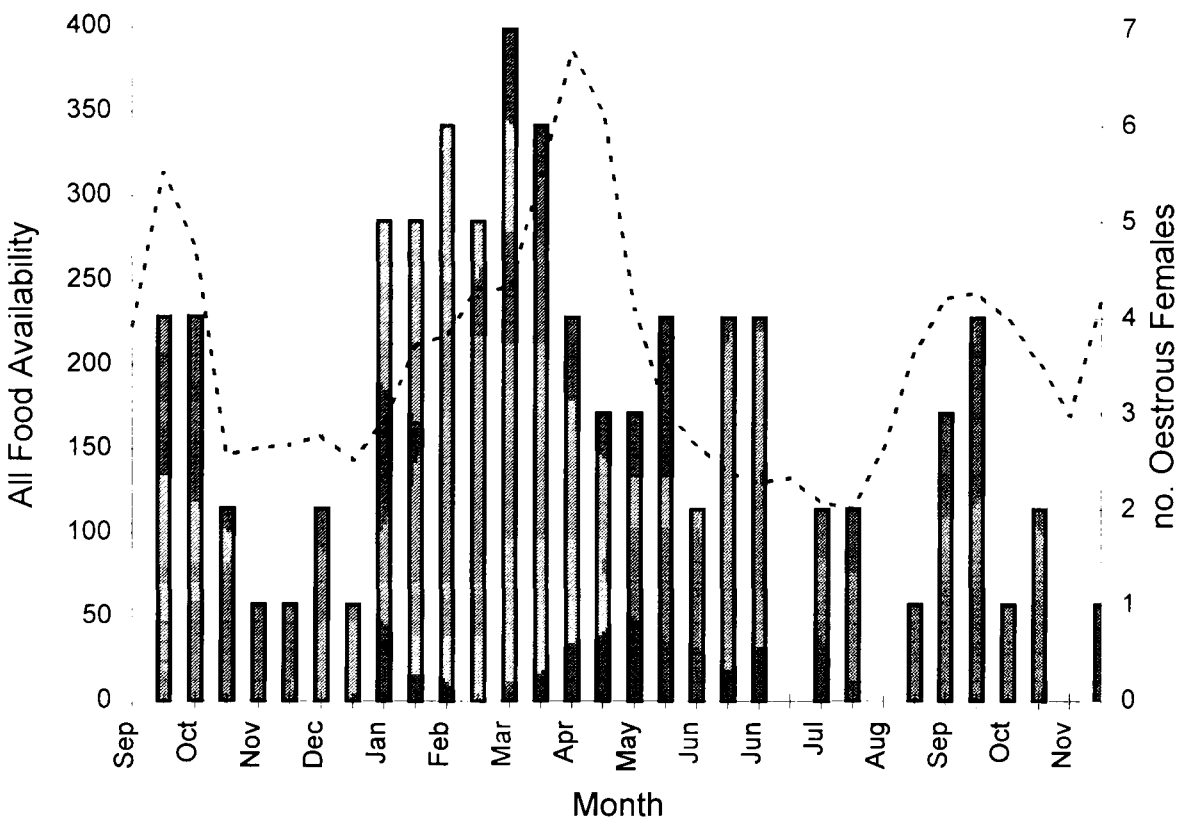


Fig 5.13 Relationship Between The Number of Oestrous Females and Measures Of Food Availability

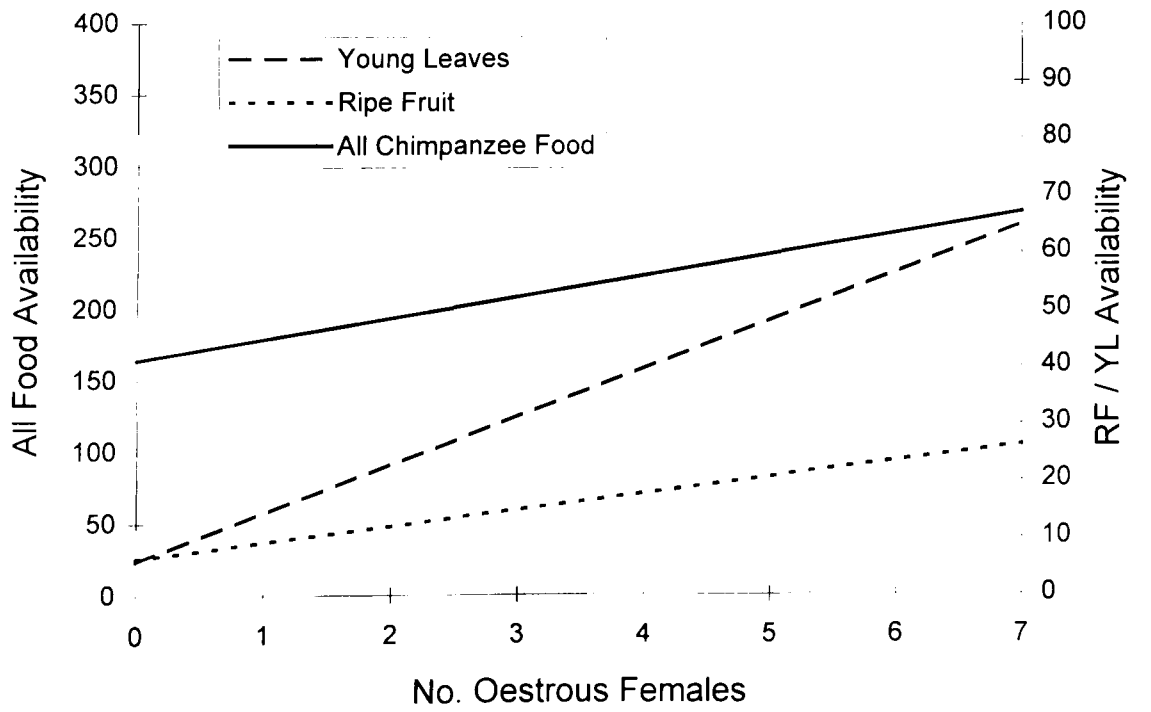


Fig 5.14 The Percentage Of Sexual Parties Containing 1-5 Oestrous Females.

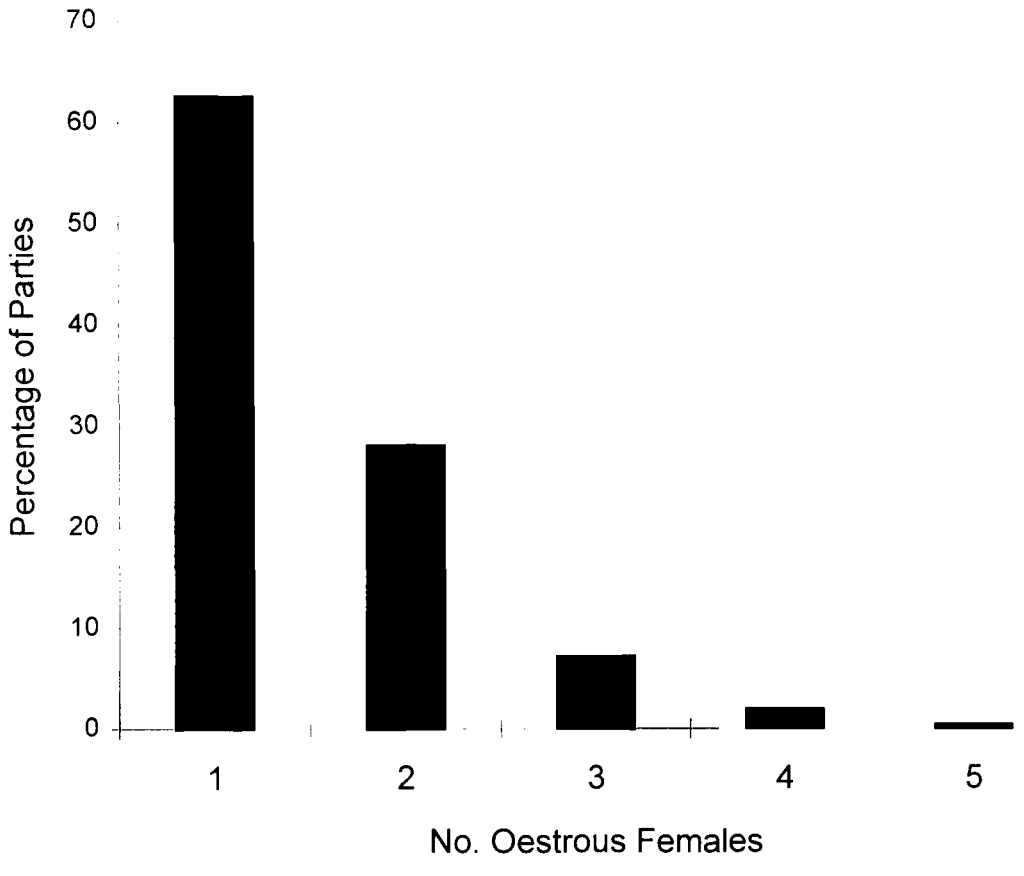


Fig 5.15 The Relationship Between The Number Of Oestrous Females In A Party And Mean Party Size.

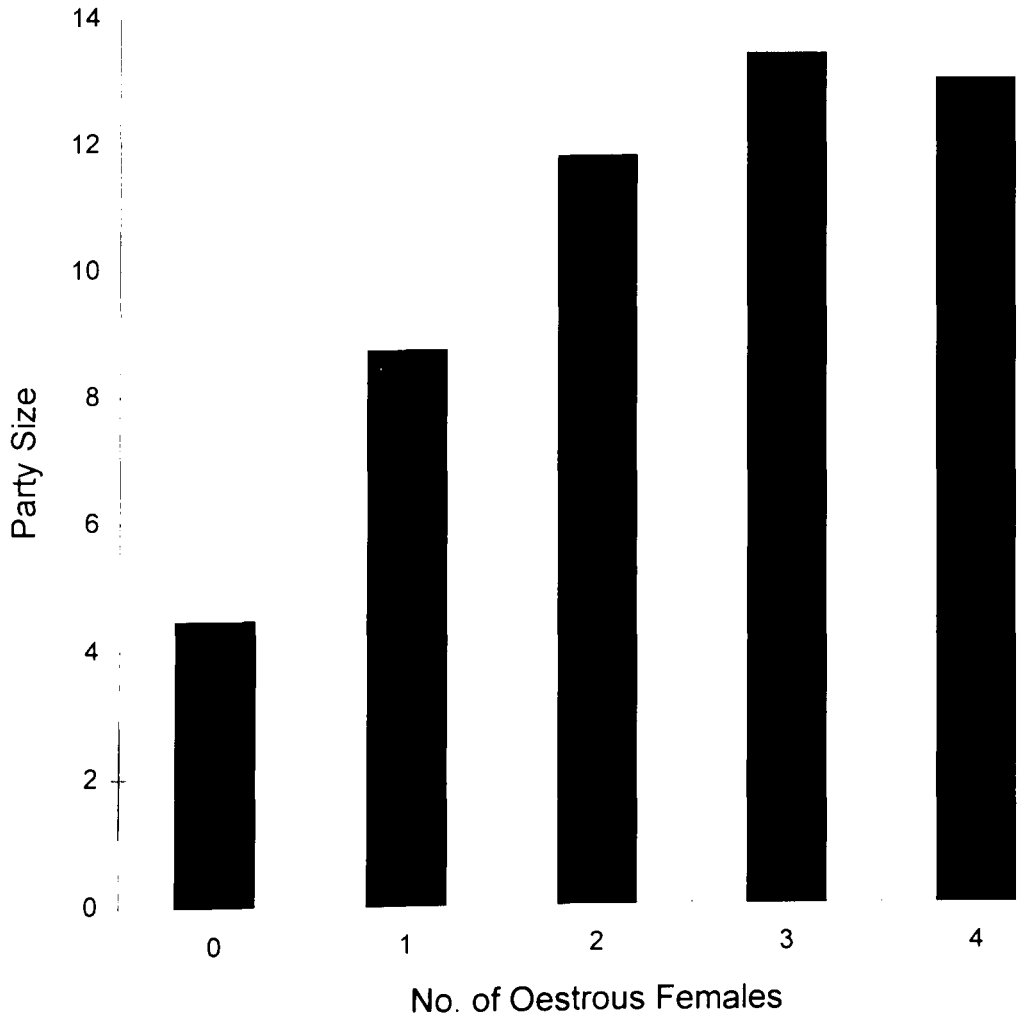


Fig 5.16 The Relationship Between The Number of Oestrous Females Available in the Community and the Size of Sexual (dashed line), Mixed (solid line) and All-Male Parties (dotted line).

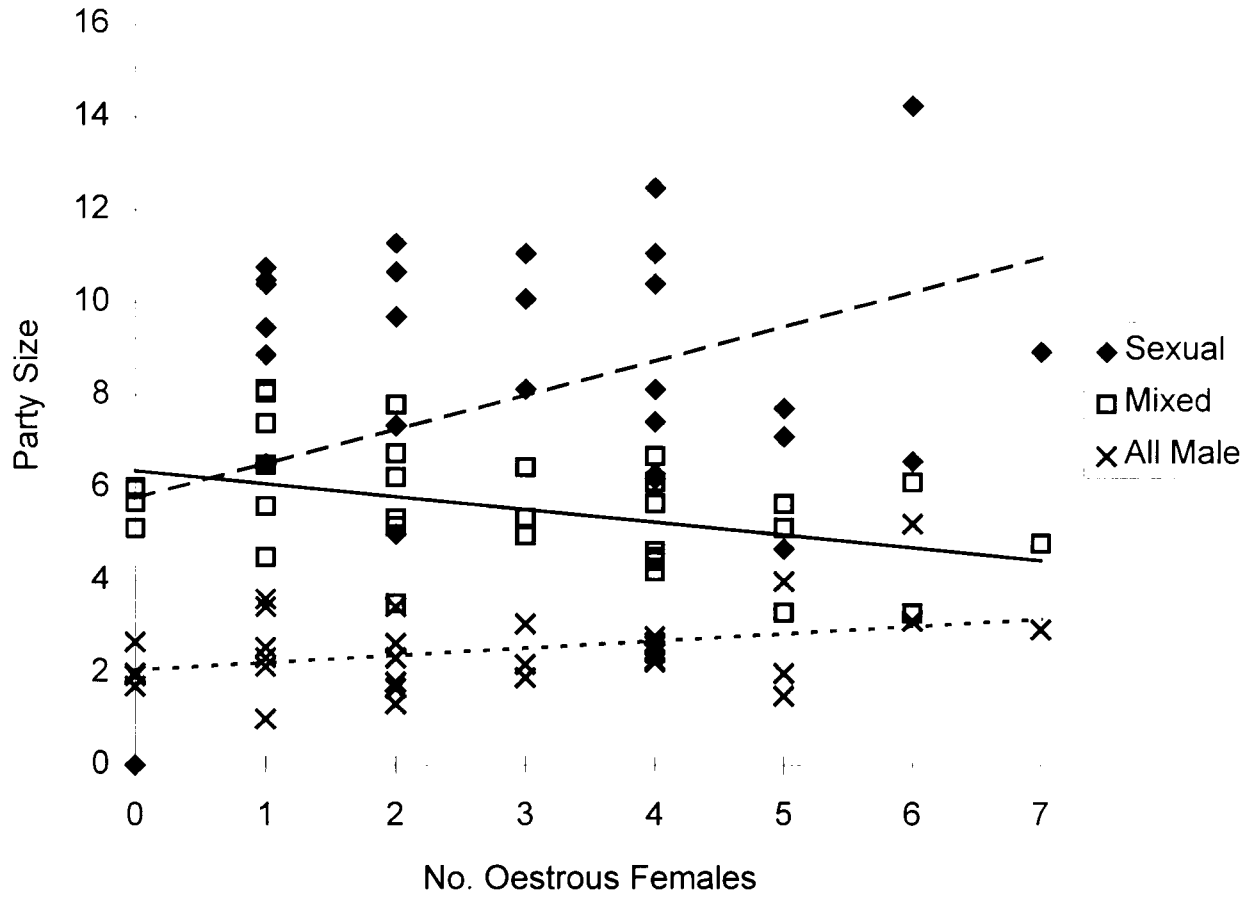


Fig 5.17 The Relationship Between Mixed Party Size and the Contributing Numbers of Males (dotted line) and Females (solid line).

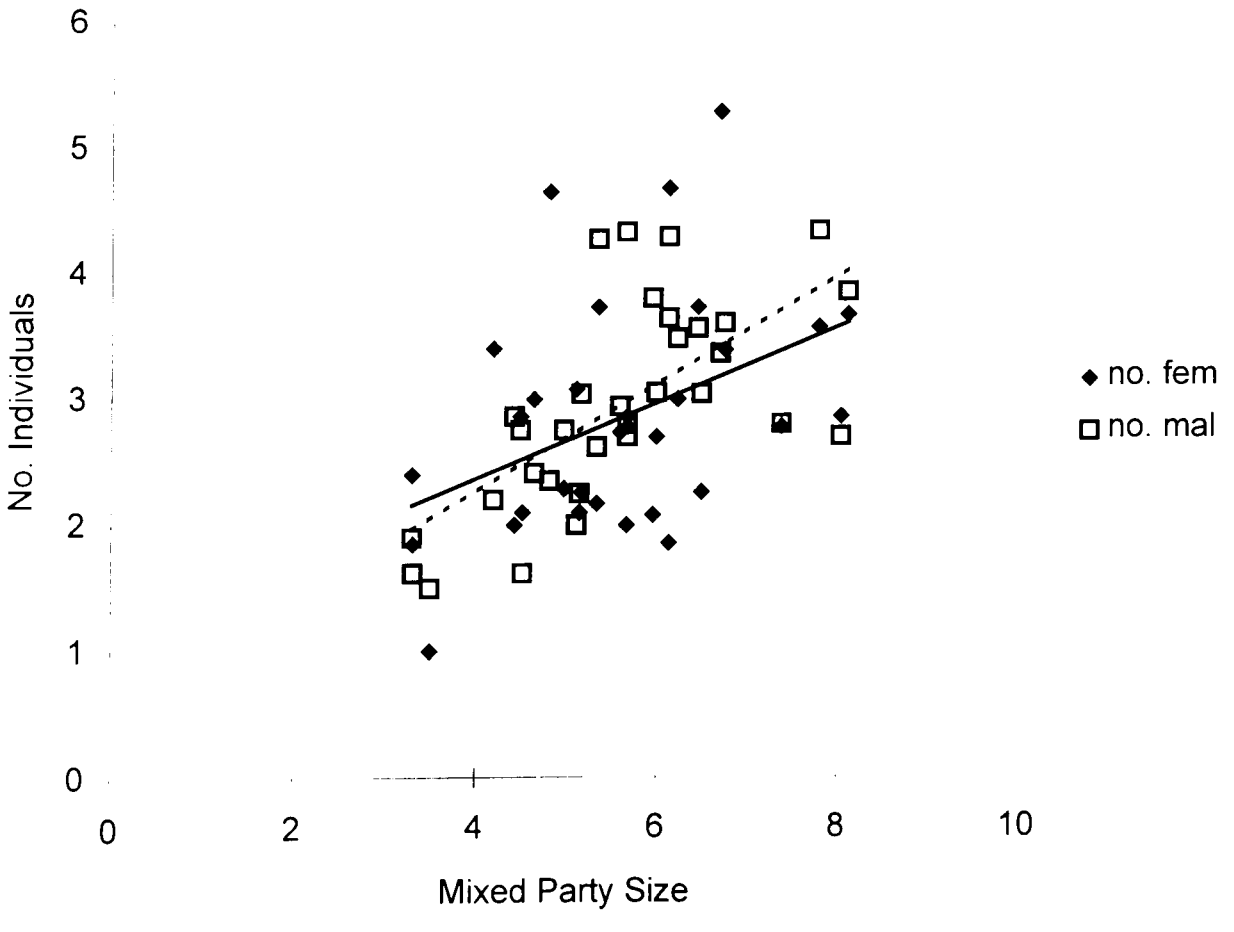
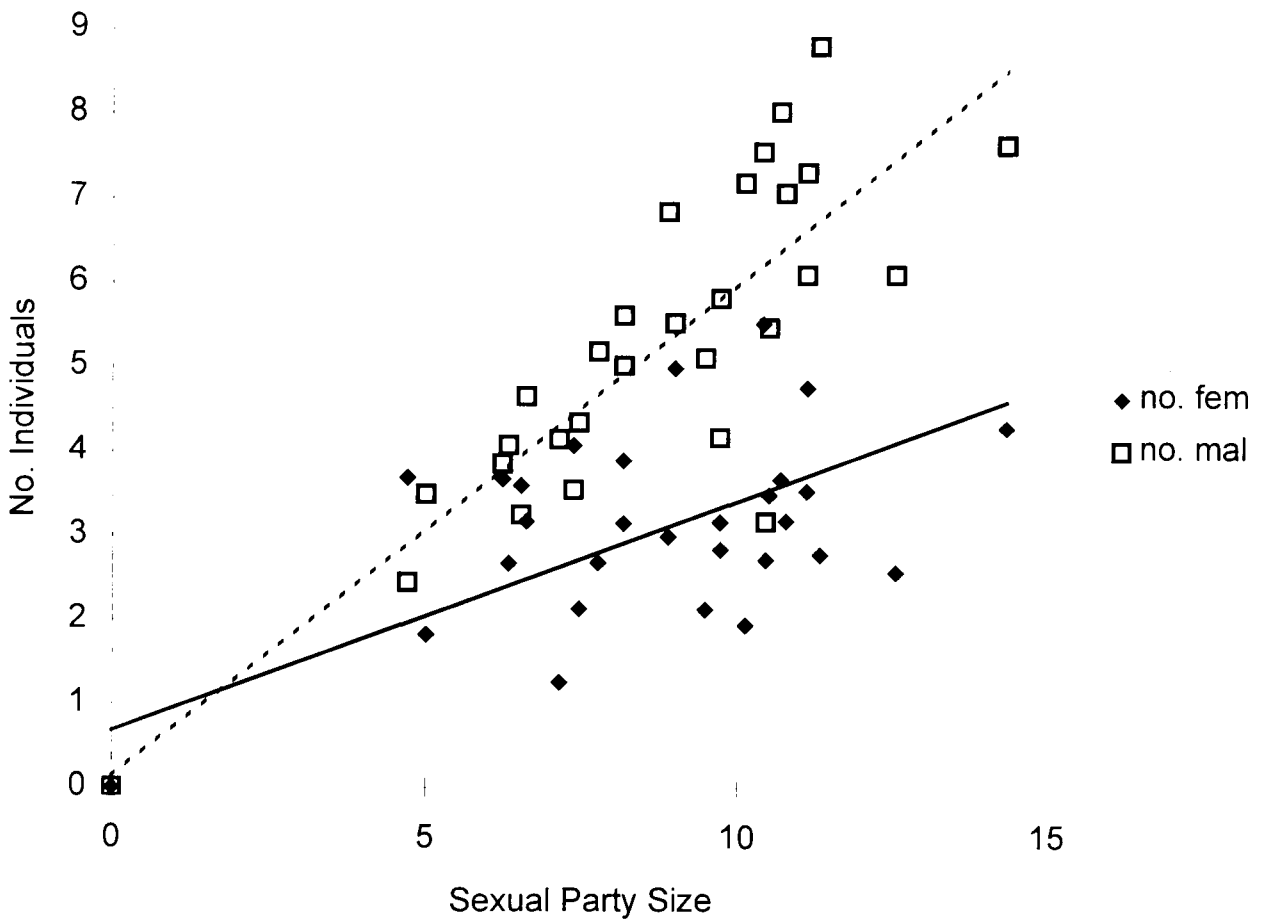


Fig 5.18 The Relationship Between the Size of Sexual Parties and the Number of Contributing Males (dotted line) and Females (solid line).



Examination of the numbers of females and males joining sexual and mixed parties shows that approximately equal numbers of males and females join mixed parties, however there is a stronger relationship between sexual party size and the number of males joining than females. This shows a stronger preference for males to join sexual parties compared to females (Fig 5.17, 5.18).

In order to look at the independent effects of food availability and the number of oestrous females on sexual and all-male party sizes, a General Linear Model was used. The various factors which were investigated as influencing grouping patterns were added to the model and removed one by one in order of explaining the least variance. These variables were the food availability measures of unripe, half-ripe and ripe fruit from both the phenology trail of chimpanzee food species and also from the community-wide sample, the availability of young leaves and the combined food availability index of all food items measured along the phenology trail. For both sexual and all-male parties, measures of food availability were stronger predictors of party size than the number of oestrous females in a two week period. For the number of oestrous females in a two week period, food availability was the best predictor

rather than any measures of party size. Within measures of food availability, the availability of young leaves was the strongest predictor. All GLM analyses accounted for covariance between factors.

ANOVA for All-male Parties:		
Food Availability Index,	$F_{1, 29} = 3.21$	p=0.084
No. Oestrous Females,	$F_{1, 29} = 1.66$	p=0.208
ANOVA for Sexual Parties		
Total Fruit Availability	$F_{1, 25} = 5.95$	p=0.022
No. Oestrous Females	$F_{1, 25} = 0.53$	p=0.475
ANOVA for number of Oestrous Females		
Young Leaf Availability	$F_{1, 27} = 11.21$	p=0.002
Ripe Fruit Availability	$F_{1, 27} = 1.13$	p=0.296

5.6 Discussion

The majority of parties observed during this study were bisexual, either mixed or sexual parties. Mixed parties are the most common party type recorded at all chimpanzee study sites (Boesch & Boesch-Achermann, 2000). During this study the sex ratio of this community approximated 1: 1 and thus the frequency of single sex and solitary party types was similar for both sexes. Boesch (1991) and Boesch & Boesch-Achermann (2000) suggest that because unisexual parties account for only one third of observed parties at Tai, the Tai community is more strongly bisexually bonded than other communities. Results from this study suggest that Budongo chimpanzees are at least as bisexually bonded as Tai chimpanzees, if not more so. It is possible that the data in this study may be biased towards parties containing females, however the procedure for the selection of male and female focal individuals attempted to minimise this bias (see chapter 3). In addition, difficulties in locating parties, as outlined in chapter 3, may have lead to a bias towards larger parties, thus under-representing the proportion of solitary individuals. However, this effect should be similar for males and females. Until it is possible to follow individual chimpanzees for the whole day from night nest to nest, the results for the frequency of different party types must remain tentative. That said, these possible

sources of bias are assumed to be constant throughout the duration of the study, thus allowing meaningful comparisons across bi-weekly periods.

The mean party size 6.36 +/-4.62SD observed during this study is well within the range of mean party sizes reported from other chimpanzee study sites. It is also the largest mean party size to be recorded from any studies so far at Budongo Forest, [5.70 +/- 3.48SD; 5.01 +/-3.57SD; 6.27 +/-4.42SD (including dependent offspring), Newton-Fisher et al. 2000]. Even accounting for the fact that different methodologies were used in some of the above studies, this demonstrates the possible variation within one study population. It is important to understand the variation in party size within one community when comparing party sizes between different sites and between species. This study also investigated the mean size of different types of party. Averages for all party types were within the ranges of mean party sizes reported by Chapman et al. (1994).

Correlations between Phenological Variables and Party Size

Party size was significantly correlated with changes in measures of food availability. In particular, the size of all-male groups and sexual parties was significantly and positively correlated with measures of food availability. Within bi-sexual groups, the number of males and females in sexual parties was significantly and positively correlated to food availability, and also the number of females in mixed groups was significantly correlated with food availability. Of all phenological measures of food availability the total food availability, incorporating not only fruit availability but also young leaf availability, was the strongest predictor of group size. Also the phenological data from known chimpanzee foods was generally a better predictor of grouping patterns than the total forest community phenological data. In conclusion, it appears that the grouping patterns of both male and female chimpanzees are affected by the availability of food resources. However, their responses to increased food availability appear to be different. In times of high food availability, males formed larger all-male parties and also there was an increase in the number of males in sexual parties. This suggests a constant benefit to grouping for males (see van Schaik, 1999). A potential benefit of grouping for males is the procurement of

mating opportunities (Wrangham, 1980; van Schaik, 1989; Sterck, 1997). Due to the fission-fusion social system and the resultant distribution of females, male chimpanzees will be better able to monopolise females if they form groups (Dunbar, 1988). The outcome of contest competition within these groups may be important for male reproductive success. All-female parties, on the other hand, did not show a significant increase in size when food availability was high. Instead, there is evidence that the number of females in bisexual parties increases, suggesting that during periods of high food availability, and presumably associated low travel costs, females maximise their associations with male group members, rather than simply with other females.

Correlation between the number of Oestrus Females, Food Availability and Party Size

The number of females in oestrus during a two week period was found to be significantly and positively correlated with measures of food availability. Although, there was a positive correlation between the mean of all party types and the number of females in oestrus, this was not significant. However, analyses of the different party types showed that the size of sexual parties and all-male parties were significantly and positively correlated with the number of females in oestrus. The group size of mixed parties is negatively correlated with the number of oestrous females available. This is presumably as an indirect result of the increase in size of all-male and sexual parties. Detailed analyses of sexual parties showed that most sexual parties contained one oestrous female and that the size of sexual parties increases as the number of oestrous females in a party increases up to a threshold limit of 3, after which there is no appreciable increase in the number of individuals in sexual parties. The mean number of males and females in sexual parties is not significantly correlated to the number of females in oestrus during a given two week period. Rather the number of males and females in sexual parties increases with the increasing availability of food. Wallis (1992, 1995, 1997) and Boesch & Boesch-Achermann (2000) have also found various reproductive parameters to be correlated with environmental seasonality. Wallis (1995) found that at Gombe, the dry season

was an important time of change for reproductive physiology. Amongst other factors the number of females exhibiting full swelling and the number of conceptions was found to be highest at this time (Wallis, 1995, 1997). In contrast, Boesch & Boesch-Achermann (2000) found at Tai that there is a peak in the number of females with full swellings during the wet season. Neither study site has detailed phenological information, so it is difficult to assess the relationship of the availability of oestrous females and food availability. Matsumoto-Oda et al. (1998) found no correlation between the availability of oestrus females and food availability, however there was a positive correlation between the size of sexual parties and food availability.

The data show that during this study period both measures of food availability and the number of oestrous females available were correlated with group size. The precise mechanism by which these two variables are operating may be complex. As both grouping patterns and the number of females in oestrus are correlated with food availability, it is difficult to know which variable may be the most influential for grouping patterns. At least two possible scenarios exist: a) increasing food availability leads to an increase in oestrous females, which in turn leads to an increase in party size; b) increasing food availability results in larger party sizes which in turn, perhaps mediated by a social or pheromonal mechanism, leads to an increased number of females in oestrus. To test these different scenarios a General Linear Model was used which suggests that food availability is independently influencing both grouping patterns and the oestrous cycles of females. The mechanism by which an increase in food availability would drive females' cycling patterns is unknown. Wallis (1995) suggested that the digestion of plant oestrogens may have an influential effect on reproductive physiology. Another theory is that during times of food richness females are able to tolerate reduced feeding time, which has been associated with being in oestrus at Mahale (Matsumota-Oda & Oda, 1998). Hunting behaviour which has been shown to influence the grouping patterns of the chimpanzee communities at Gombe and Tai (Stanford et al., 1994; Boesch & Boesch-Achermann, 2000), was not observed during this study and therefore did not influence party size.

Seasonal variation in chimpanzee party size, assumed to be associated with variations in food resources, has been documented from other chimpanzee study sites (Bossou: Sakura, 1994; Tai: Boesch, 1996; Doran, 1997; Mahale: Nishida, 1979; Gombe; Wallis, 1995; Stanford et al., 1994; Kibale: Wrangham et al., 1991, 1992). The results of this study, however, differ from the results of a previous study at Budongo which found that although there was a positive relationship between food patch size, as indexed by DBH, group size was weakly and possibly negatively correlated with overall food availability (Newton-Fisher et al. 2000). It was suggested that the food supply may have been exceptionally rich during the four years of that study, and that in times of a superabundance of food, individuals would choose to form smaller parties in order to concentrate on alliance formation (see Newton-Fisher, 1997). It was also suggested that the absence of a positive relationship between food availability and group size may be a result of small sample sizes of some important fruiting trees along the phenology trails. In addition, the availability of young leaves was not recorded. In the present study the phenological variable which most consistently predicted grouping patterns was the index of total food availability. This incorporates the food availability index of young leaves, fruit, buds and flowers. Chapter 6 highlights the importance of young leaves in the Sonso chimpanzee diet and in particular, the preference for young leaves rather than fruit at certain times of year. Furthermore, although this study concerned the same community of chimpanzees, it used a different phenology trail. The collection of phenology data was designed specifically with the aim of relating the information to chimpanzee behaviour. It covered a representative area of the community home range and also a representative cross-section of the different habitat types. With the exception of the variable of community-wide availability of ripe fruit, all other phenological variables which were significantly and positively correlated to aspects of group size were variables measured along the phenology trail of chimpanzee food species.

Unfortunately, data on the temporal variation of group size are not presented in Newton-Fisher et al. (2000), however, the data on the temporal variation of group size presented in Newton-Fisher (1997) show a major peak in group size occurring in

March. This corresponds to data collected during this study. Thus, although Newton-Fisher (1997) states that there is no clear seasonal pattern in grouping patterns, there does appear to be some relation between the data in the two studies. This underscores the importance of collecting appropriate detailed phenological data in order to investigate the relationship between food availability and chimpanzee behaviour.

Ecological theory predicts that females distribute themselves in relation to food resource distribution, and that in turn males distribute themselves according to sexual opportunities. The results of this study suggest that females are also attracted to males, as the number of females in mixed and sexual parties increased with increased food availability, whereas the size of all female parties did not. It is possible that either the increase in food availability and the consequent low travel costs, or the temporary nature of these benefits, were not sufficient to make female alliances and resource defence profitable. It is unclear how females may gain ecological benefits from associating with males, therefore it is suggested that females are increasing their association with males in order to gain social benefits. In contrast to the predictions of ecological theory, male behaviour was also heavily influenced by the temporal availability of food resources. In addition, the number of sexual opportunities were positively related to the availability of food. It appears that food availability is determining both grouping patterns and the availability of oestrous females.

5.7 Conclusions

- Party size was significantly correlated with changes in measures of food availability; in particular the size of all-male and sexual party types.
- The size of all-female parties was not correlated with any measure of food availability. However, within mixed groups the number of females in a party is significantly correlated to measures of food availability. Therefore it appears that, during periods of high food availability and corresponding low travel costs, females maximise their associations with male group members, rather than with other females

- The number of females exhibiting maximum oestrous swelling during a two week period was found to be significantly and positively correlated with measures of food availability
- The size of sexual and all-male parties was significantly correlated with the number of oestrous females
- GLM ANOVA show that food availability is a stronger predictor of group size than the number of oestrous females
- The number of oestrous females was predicted more strongly by food availability than by group size.
- This suggests that levels of food availability independently determined both the size of parties and the oestrous cycles of females

Chapter 6

Feeding Behaviour and Activity Patterns

6.1 Introduction

Chapter 4 outlined changes in food availability in the plant community, chapter 5 then investigated the effect of food availability on the grouping patterns of the chimpanzee community. This chapter will address how these changes in resource availability are expressed in the diet and activity patterns of the chimpanzees. The degree of variation in food availability has been suggested as one possible factor influencing the differences in social organisation between bonobos and chimpanzees (Malenky 1990, cited in Chapman et al., 1994). In addition, the differences in social organisation or degree of bonding between the sexes within *P. troglodytes* may be the result of variations in food availability between different sites. However, few study sites have detailed phenology, diet and social behaviour records. Previous studies of chimpanzee diet at Budongo have suggested that the Sonso community does not experience a period of severe food shortage (Newton-Fisher, 1999b). This study hopes to address this suggestion by the comparison of quantitative measures of both food availability and chimpanzee diet. Seasonal variation in activity patterns will also be examined. In addition, comparisons of activity budgets and diet between the sexes and life history categories are necessary in order to address factors affecting association and grouping patterns

Diet

Primate diets may be broadly classified into 3 major categories depending on the major food item; frugivores, folivores, insectivores. On the basis of these classifications, chimpanzees have been described as frugivores (Wrangham 1977; Nishida & Uehara, 1983; Ghiglieri 1984; Goodall, 1986; Isabirye-Basuta, 1989; Wrangham et al., 1991; Sugiyama & Koman, 1992). However, although the major

component of the diet is fruit, significant proportions of leaves, insects, seeds, flowers and mammalian prey have also been described as contributing to the diet. Feeding on fruit pulp alone will not provide a complete diet. *Fruits* are typically rich in simple sugars but deficient in protein and fats. Therefore, all frugivorous primates must supplement their diet of fruit with insects or leaves or both. The choice of food items in an animal's diet will have important implications for ranging and association patterns. For example, Oates (1987) described a general negative relationship between the proportion of time an individual spent moving and the proportion of foliage in the diet. The fission-fusion social organisation of large bodied frugivores may be an adaptation to a highly dispersed food source. Plants which invest in fleshy fruit do so in order to attract potential seed dispersers and therefore should be relatively easy for the consumer to find. However, these fruiting trees are often highly dispersed within the forest which results in frugivorous primates having to cover larger areas, in the process acting as seed dispersal agents, in order to maintain a relatively fruit-rich diet compared to most folivores. *Seeds* are higher in fats, proteins and minerals than fruits. Although a frugivore may ingest a large quantity of seeds whilst eating fruit pulp, these usually contain physical defences against digestion, thus allowing the seed to be dispersed by the primate. Alternatively, primates may extract seeds before ingestion. Some primates are capable of surviving for long periods of time on seeds alone, whereas no species of primate is known to feed only on fruit pulp (Janson & Chapman, 1999). Seeds also may be available over longer periods of time than fruit pulp, which is timed to ripen at the most appropriate time for seed dispersal and subsequent germination. *Flowers* are also a source of simple sugars, but the nectar is usually a dilute source of simple sugars compared to fruit pulp. Therefore, they are generally used as a fall back food when little fruit is available. *Leaves* are a rich source of protein and sugars, however difficulties arise in the problem of digesting cellulose and also many leaves contain toxic chemicals even when young. Therefore a primate must have specific mechanisms for dealing with cellulose digestion or toxic chemicals, as in the colobines, or it must restrict its diet to the poorly defended species or food parts. For fruit-eating primates, the importance of leaves in the diet is to provide protein rather than sugar. *Insects* can

provide nearly all essential nutrients and are relatively easy to digest. The problem is the chitinous exo-skeleton which is both physically hard to feed upon for smaller primates and difficult for all to digest. Primates which eat mainly fruit but supplement their diet with insects generally avoid ingesting the chitin exoskeleton (Janson & Boinski, 1992, cited in Janson & Chapman, 1999). Larger primates have a correspondingly larger metabolic demand, therefore as body size increases the time spent feeding on insects must increase, and thus the importance of insects in the diet will decrease (Janson & Chapman, 1999).

The different sexes and life history groups may have different nutritional requirements. Lactating females will have higher protein and mineral requirements than non-lactating or similar-sized males. Seasonal changes in food distribution are probably an important factor in many of the instances where primates are found to have a distinct breeding season (Lancaster & Lee 1965, cited in Oates, 1987), e.g. male squirrel monkeys lay down fat before the breeding season.

Response to Food Scarcity

If animals are selecting food items according to an optimal foraging model, the more common the food with the highest nutritional value, the fewer lower-quality foods the animal needs in its diet. Thus it follows that the scarcer food is, the more diverse the diet will be. When there is a reduction in the availability of food, non-migratory animals may either increase the time spent searching for food, or reduce selectivity and feed on a broader range of lower quality food items. Oates (1987) summarised the available evidence and showed that in times of food scarcity species which rely on fruit will usually increase the time spent searching for food, whereas species which rely on foliage will decrease their level of activity in an effort to minimise energy expenditure. Some studies of great apes support this argument. Yamagiwa (1999) showed the differing response of gorillas and chimpanzees to decreases in fruit availability. Whereas gorillas changed diet and decreased day range, chimpanzees maintained their frugivorous diet and expanded their range. Tutin et al. (1997) also state that chimpanzees maintained a fruit-dominated diet during the annual dry season and associated period of food scarcity. The chimpanzees fed on the

oil palm, which was described as fruiting asynchronously and was therefore available at all times. It is unclear how the chimpanzees in Lopé adjusted their activity patterns in response to the decline in food availability. The chimpanzees at Gombe also concentrate feeding activities on the fruit of the oil palm during the dry season, (a period of presumed food scarcity), (Stanford, pers. comm.). Doran (1997), studying the Tai community of chimpanzees during a period of food scarcity, also found that the community spent both more time feeding and fed on lower quality food items. They were also recorded to reduce their day range and party size. At Kibale Forest the chimpanzees also turn to lower quality food items by increasing the amount of THV in their diet during times of food scarcity (Wrangham et al., 1991). Piths typically have low sugar and protein levels. The intake of leaves in the diet was not influenced by fruit abundance. Wrangham et al. (1991) suggest that the chimpanzees are feeding on pith in times of low food availability as a source of energy in the form of fermentable fibre rather than for its protein content. When succulent fruit was scarce at Lopé, both chimpanzees and gorillas increased their consumption of THV in the families of Marantaceae and Zingiberaceae. Nutritional analyses found the pith of certain species to contain significant quantities of sugar (Rogers et al., 1990). The sugar content of Aframomum spp. was found to vary spatially between different clumps and also temporally between seasons; initial analyses suggest that sugar content is higher in the dry season (White et al., 1995). Thus, at Lope chimpanzees may be obtaining a source of sugar from pith during the period food scarcity.

Isabirye-Basuta (1989) assessed the diet of chimpanzees at Kibale with respect to the model of optimal foraging. As predicted the number of plant species utilised each month was negatively related to fruit availability and the monthly proportion of leaves in the diet correlated with dietary diversity. However, the chimpanzees did not utilise the various plant species in proportion to their abundance. It is necessary to have information on plant chemistry, digestibility and handling times before we can further test the optimality models.

Dietary responses to periods of food shortage are important in order to understand the ranging and association patterns of a community. In addition,

knowledge of keystone species and species which depend on chimpanzees, for seed dispersal may be needed for forest management plans.

Cultural Diversity

Differences in the use of plant species as food items have been recorded from two nearby sites in Tanzania. Nishida et al. (1983) list 16 different foods from nine plant species present in both study areas which are eaten regularly at Mahale, and are either ignored or only eaten in small quantities at Gombe. Likewise, 6 different foods from 3 species which are eaten regularly at Gombe have not been seen to be eaten at Mahale. Although recorded as being present at both sites, it is possible that the density and distribution of some plant species may be different, so a species which is valued at one site is not at another. However, in light of recent evidence of differences in both material and behavioural cultures between different study populations of the same sub-species (Whiten et al., 1999), it is interesting to note differences in diet between sites. It is important to have information from ape communities studied in a wide range of habitats in order to distinguish between site-specific and species-specific traits. In addition, it is interesting to study the feeding behaviour of forest-living chimpanzees in areas where they are not sympatric with gorillas, in order to address issues of competition between apes.

6.2 Aims

- to examine the response of the Sonso community of chimpanzees to changes in food availability in terms of activity patterns and diet.
- to investigate sex and life history differences in activity patterns and diet choice in order to understand differences in ranging and association patterns.

6.3 Methodology

Activity budget and feeding behaviour data were analysed for the period January - December 1998. This was the period where 30 min focal samples were carried out on both male and female chimpanzees (see General Methodology, chapter 3). With this change in recording methods there was also a slight change in the checksheet to record the activity of all party members (previously only the activity of the focal individual had been recorded). An individual's activity, and also food species and food item if feeding, were recorded every 15 min during instantaneous scan sampling as described in the General Methodology chapter. Data were collected on all independent individuals and were classified into the following sex and life history categories: All-Males (n=17), All-Females (n=19), Adult Males (n=12), Adult Females (n=12), Adolescent Males (n=4), Adolescent Females (n=6), Cycling Females (n=8), Non-Cycling Females (n=10). Cycling females were all females which exhibited a full oestrous swelling during the course of the study, thus data were collected on these females both when the were exhibiting a full swelling and when they were flat. The behaviour of reproductive cycling females has been shown to be significantly different from that of non-cycling females regardless whether or not they are exhibiting a sexual swelling (Matsumoto-Oda, 1999). The total number of data points for all independent individuals used to assess activity budgets was 15, 589. Of these, 7,874 were used for the analyses of feeding behaviour (see Appendix C.1 & C.2 for distribution of these data throughout the year and across individuals).

Since sample days and scans within days are not statistically independent, both the activity and diet data were analysed by pooling scores for each sample period and calculating the proportions of time spent feeding etc. from the total number of scores for that period. The diet and activity budgets were analysed in time blocks which correspond to the two week phenology sample periods. The results of both activity budgets and feeding behaviour were correlated with the corresponding phenology sample periods (n=25). The first of these time periods falls within the phenology period labelled Dec 97, (see Chapter 4).

Activity Budgets

The activity categories listed in the methodology section were collapsed into 5 major categories:

FORAGE: includes all behaviour involved in the direct processing and ingestion of food

GROOM: all grooming activities

REST: all resting activities

MOVE: all travel activities, both on the ground and within the trees.

SOCIAL: all other behaviours, e.g. copulation, dominance, vocalisation.

For the purposes of this study all *MOVE* behaviours are assumed to be primarily associated with the search for food. It is likely that not all travelling behaviour is exclusively involved in the search for food but may be combined with other activities, for example territorial patrolling or searching for mates. In practice, it is difficult to differentiate these activities, so, as the search for food is the most important activity for an individual, all travelling activity is classified as the search for food.

Diet

Dietary data were analysed using two different methods to calculate the relative importance of different food items in the diet: the time the chimpanzees were observed to spent feeding and the analyses of faecal content. Early months of field observations, (prior to January 1998), suggested that due to visibility and habituation problems, feeding observations may be biased to arboreal feeding activities. In addition, on occasions the chimpanzees had been observed to feed on the ground on terrestrial vegetation, THV. The inclusion of terrestrial herbaceous vegetation (THV) in the diet may be important in influencing the response to resource scarcity and the resulting grouping patterns. As a result the aim of collecting dung samples was to quantify the importance of pith in the diet and also to confirm feeding data collected through observations. The occurrence of seeds in the dung also gives general information on seed dispersal.

For analyses of faecal data with both phenology and feeding observations, all data were combined into 4 week blocks due to the lack of dung samples in some 2 week phenology periods.

A list of food species and food items was determined using data from both instantaneous scan sampling and *ad libitum* records. Important species in the diet were identified as those which accounted for greater than 0.5% of feeding time. In addition, a Rank Preference index (Kaplin, 1998), was calculated for the 12 principle food species. This index takes into consideration the proportion of time spent feeding on each food species and the availability of that food species each month.

$$t_i = r_i - s_i$$

t_i = Measure of relative preference
r_i = Rank usage of resource type I (I = 1,23,...., m) each month.
s_i = Rank of availability of resource type I (food availability) each month

The mean values over the study period were used to determine the Preference Rank index. Only food species and not food items were included in these analyses to give an idea of the important species in the diet.

Dietary diversity during each phenology period was measured by using both a count of the number of species consumed and standardised Shannon-Wiener indices (Oates, 1977; Krebs, 1989, cited in Newton-Fisher, 1999b). The standardised Shannon-Wiener diversity indices take into account the relative proportion of each species in the diet.

$$J' = -[\sum (p_i) (\log 2\ p_i)]/ \ln n]$$

where n = number of species

p_i = proportion of the ith species in the diet each month.

6.4 Analyses

All analyses were performed using Minitab version 12 and SPSS version7.5. Mann-Whitney tests were used to compare differences in diet and activity patterns between the different sex and life history classes. Minitab expresses this test statistic as W. Spearman rank correlations were used to investigate relationships between dietary, activity and phenology patterns. This test statistic is r_s.

6.5 Results

Overall Activity Budget

Analyses of all independent individuals (N=36) for the whole study period (Jan 98 - Dec 98) showed that the majority of time was spent feeding and in other activities associated with the direct ingestion of food (see Fig 6.1).

Fig 6.1 Average Time Spent Performing Each Activity For The Whole Community Over The Course Of This Study, (standard error shown in brackets).

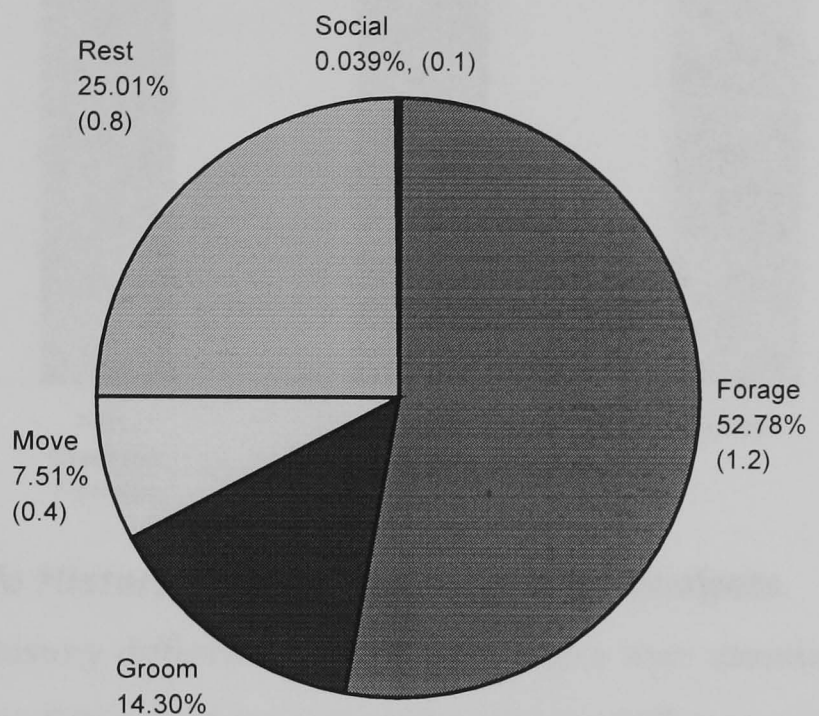
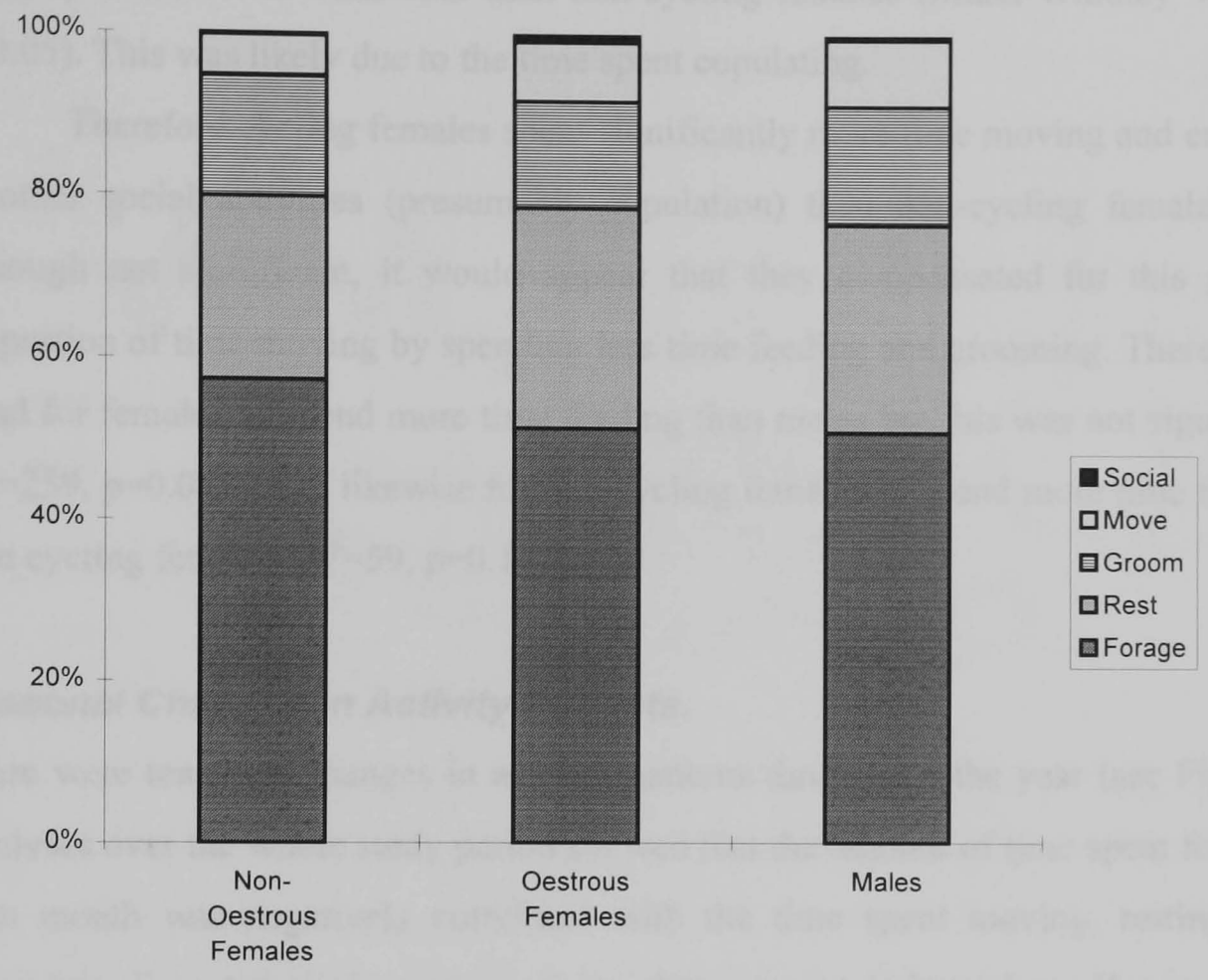


Table 6.1 Mean Percentage of Time Spent on Each Activity For The Different Male and Female Life History Classes with Standard Error Shown Below Each Entry in Italics.

	N	Forage	Groom	Move	Rest	Social
All-Males	**17**	**50.60**	**14.76**	**08.83**	**25.49**	**0.033**
		1.4	*1.3*	*0.4*	*0.9*	*0.0*
All-Females	**19**	**54.73**	**13.90**	**06.33**	**24.58**	**0.046**
		1.9	*1.0*	*0.5*	*1.3*	*0.1*
Adult Males	**12**	**48.97**	**16.81**	**08.37**	**25.56**	**0.030**
		1.6	*1.4*	*0.5*	*1.1*	*0.1*
Adolescent Males	**4**	**54.68**	**11.31**	**09.67**	**23.90**	**0.044**
		1.9	*1.6*	*0.2*	*1.8*	*0.1*
Adult Females	**12**	**56.31**	**15.19**	**05.35**	**22.00**	**0.035**
		2.6	*1.1*	*0.5*	*1.5*	*0.2*
Adolescent Females	**6**	**51.57**	**12.14**	**07.38**	**28.21**	**0.070**
		3.1	*2.2*	*0.8*	*1.9*	*0.2*
Cycling Females	**8**	**51.49**	**13.17**	**07.34**	**27.20**	**0.080**
		2.1	*2.0*	*0.6*	*1.7*	*0.3*
Non-Cycling Females	**10**	**57.33**	**14.98**	**04.98**	**22.53**	**0.019**
		3.1	*1.1*	*0.6*	*2.0*	*0.1*

Fig 6.2 A Comparison Of The Percentage Time Spent Pursuing Each Activity For All Males, Cycling Females And Non-Cycling Females.



Sex and Life History Differences in Activity Budgets.

Sex and life history differences in activity budgets were examined (see table 6.1 and Fig 6.2). Mann-Whitney tests were used to test for differences in the medians of time budgets between the different age and sex classes. The following comparisons were made for each activity category: All-Males vs All-Females, Adult Males vs Adult Females, Adult Males vs Adolescent Males, Adult Females vs. Adolescent Females, and Cycling vs. Non-Cycling females.

There were significant differences between the medians of all-males vs all-females in the time spent moving. Males were found to spend significantly more time moving than females (Mann-Whitney $W=405$, $p<0.01$), and cycling females spent significantly more time moving than non-cycling females (Mann-Whitney $W=104$, $p<0.01$). Adolescent females were found to spend more time resting than adult females (Mann-Whitney $W=88$, $p<0.05$). In addition, there was an almost significant difference between the amount of time spent resting between cycling females and non-cycling females, with cycling females spending more time resting (Mann-

Whitney W=98, $p<0.05610$). Cycling females also spent more time engaged in the category other social behaviour than non-cycling females (Mann-Whitney W=100, $p<0.05$). This was likely due to the time spent copulating.

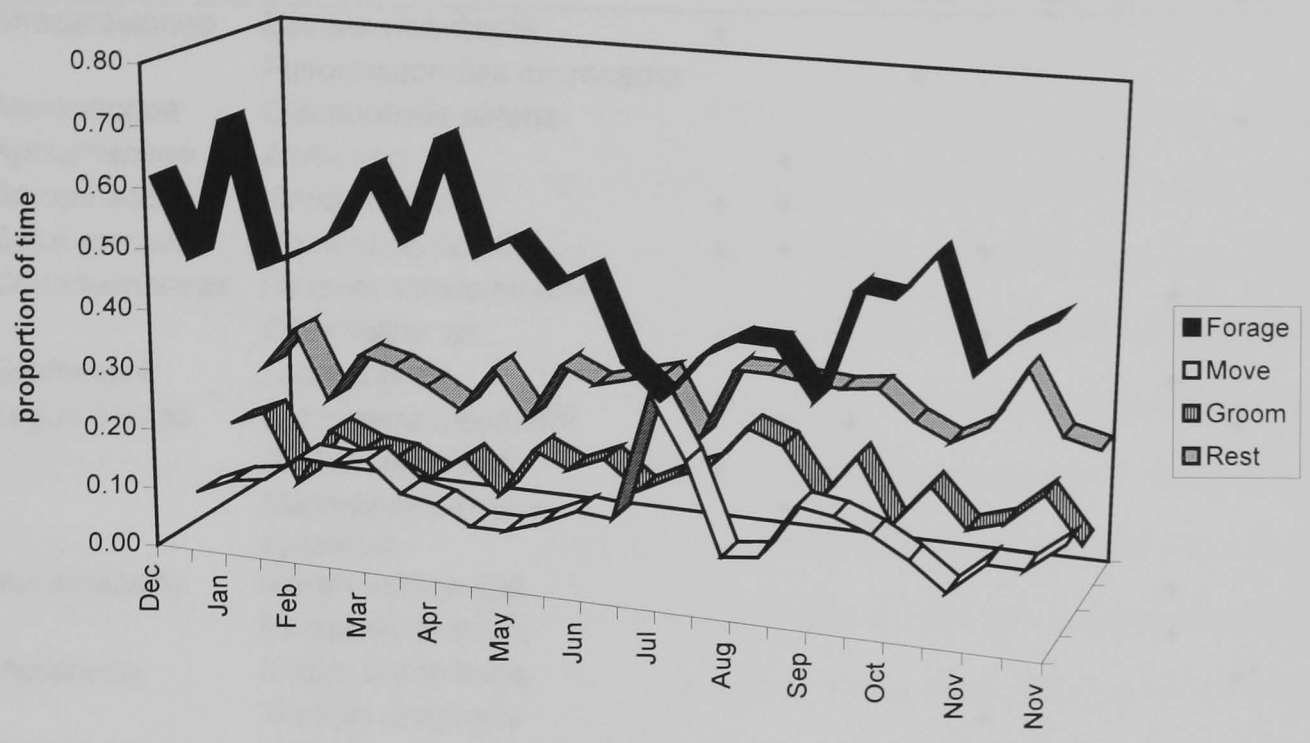
Therefore cycling females spent significantly more time moving and engaged in other social activities (presumably copulation) than non-cycling females, and although not significant, it would appear that they compensated for this greater proportion of time moving by spending less time feeding and grooming. There was a trend for females to spend more time feeding than males but this was not significant (W=259, p=0.081); and likewise for non-cycling females to spend more time feeding than cycling females (W=59, p=0.142).

Seasonal Changes in Activity Budgets.

There were temporal changes in activity patterns throughout the year (see Fig 6.3). Analyses over the whole study period showed that the amount of time spent foraging each month was negatively correlated with the time spent moving, resting, and grooming. For statistical purposes these data are not independent. However, the results are of biological significance and therefore included.

Activity patterns were then correlated with measures of food availability. The proportion of time spent foraging was found to be significantly positively correlated with the availability of young leaves (r_s=0.564, $p<0.01$) and the combined measure of all food availability (r_s=0.606, $p<0.001$). The proportion of time spent moving and engaging in other social behaviour other than grooming, was not significantly correlated to any measure of food availability. The time spent resting was significantly and negatively related to the combined measure of the availability of all chimpanzee food parts (r_s= -0.479, $p<0.05$) and availability of young leaves (r_s = -0.474, $p<0.05$), as was also the amount of time spent grooming (all-food r_s = -0.542, $p<0.01$; young leaves r_s = -0.525, $p<0.01$). In addition, the time spent resting was significantly and negatively related to the availability of cycling females (r_s = -0.430, $p<0.05$).

Fig 6.3 Temporal Changes in Activity Budgets for all Independent Individuals.



Therefore, it would appear that when food is scarce chimpanzees spend more time resting and moving. The amount of time spent grooming is also negatively related to food availability further illustrating the important effect of ecology on social relationships

General Feeding Behaviour

A total of 49 plant food species and 91 plant food items were recorded during scan sampling and *ad libitum* data collection (see Table 6.2). In addition, caterpillars, lichen, soil and the seeds of *Calconcoba schweinfurthii* were found in dung samples. The chimpanzees were also observed to eat termites and honey. During the period of data collection before January 1998, there were two observations of feeding on mammalian prey, (black and white colobus and blue diuker). On both occasions no hunting behaviour was observed, and in the case of the blue duiker it was likely to have been obtained opportunistically. There were no feeding remains of mammalian prey in the faecal samples.

Table 6.2 List Of Plant Food Species And Items Recorded During Scan Sampling. (RF = ripe fruit, UR = unripe fruit, SE = seeds, ML = mature leaves, YL = young leaves, BU = buds, FL = flowers, PH = pith, BK = bark, RW = rotten wood. ? = unknown, * = resin).

Family	Species	RF	UR	SE	ML	YL	BU	FL	PH	BK	RW
Anacardiaceae	*Lannea welwitschii*	+									
	Pseudospondias microcarpa				+						
Annonaceae	*Cleistopholis patens*									+	+
Apocynaceae	*Alafia* spp.		+								
Boraginaceae	*Cordia millenii*	+	+								
Cecropiaceae	*Myrianthus holstii*	+	+			+					
Commelinaceae	*Palisota schweinfurthii*								+		
	Commelina sp.					+					
Gramineae	*Leptaspis sp.*								+		
Leguminosae	*Cynometra alexandrii*		+	+		+				+	
	Dialium excelsum	+									
	Mildbraediodendron excelsum		+								
Marantaceae	*Marantochloa spp..*								+		
	Megaphrynium sp.								+		
Meliaceae	*Khaya anthotheca*									+*	
	Trichilia dregeana					+					
Moraceae	*Antiaris toxicaria*	+				+					
	Broussonetia papyrifera	+	+			+	+	+			
	Ficus barteri	+									
	Ficus exasperata		+		+	+				+	
	Ficus mucuso	+	+								
	Ficus natalensis	+	+								
	Ficus ottoniaefolia	+	+								
	Ficus polita	+	+								
	Ficus sansibarica	+	+							+	
	Ficus saussureana	+	+							+	
	Ficus sur	+	+							+	
	Ficus vallis-choudae	+				+					
	Ficus variifolia	+	+			+					
	Milicia excelsa	+	+								
	Morus lactea	+									
Palmae	*Raphia farinifera*								+		
Piperaceae	*Piper guineense*								+		
Polypodiaceae	*Platycerium angolense*				+	+					
Rhamnaceae	*Lasiodiscus mildbraedii*					+					
	Maesopsis eminii	+									
Rutaceae	*Balsamocitrus dawei*	+									
Sapotaceae	*Chrysophyllum albidum*		+								
	Chrysophyllum gorungosanum	+									
	Chrysophyllum perpulchrum	+									
Sterculiaceae	*Cola gigantea*									+	
Tiliaceae	*Desplatsia dewevrei*	+	+								
Ulmaceae	*Celtis durandi*					+					
	Celtis mildbraedii					+		+			

Table 6.2 continued.

Family	Species	RF	UR	SE	ML	YL	BU	FL	PH	BK	RW
Ulmaceae	*Celtis wightii*					+		+			
	Celtis zenkeri					+					
Urticaceae	*Urera camaroonensis*					+		+			
Zingiberaceae	*Aframomum* spp.	+							+		
?	unknown climber spp.				+	+					

Table 6.3 lists the species which accounted for more than 0.5% of all feeding records. The data compare well to that of Newton-Fisher (1999b). Both field studies recorded a similar number of species which were fed upon for >0.5 % of feeding time (19 spp. Newton-Fisher, 199b), however there were interesting differences in the species included in the lists. Both studies recorded the same top 3 food species, *F.sur, B. papyrifera, F.mucuso*; however seven of the other species recorded by Newton-Fisher were not recorded as accounting for >0.5% of feeding time during this study (*Maesopsis eminii, Celti durandi, Khaya anthotheca, Cleistopholis patens, Raphia farinifera, Ficus natalensis*). Three of these species were not recorded during scans for the whole of this study period (*Croton macrostachys, Maesopsis eminii, Celtis durandi*). This demonstrates the flexibility in the chimpanzee diet, possibly as a result of a fluctuating phenology patterns. The top three species together account for 61.68% of the total feeding time. They are all members of the same family Moraceae. *Brousonnetia papyrifera*, is an exotic species planted by the sawmill.

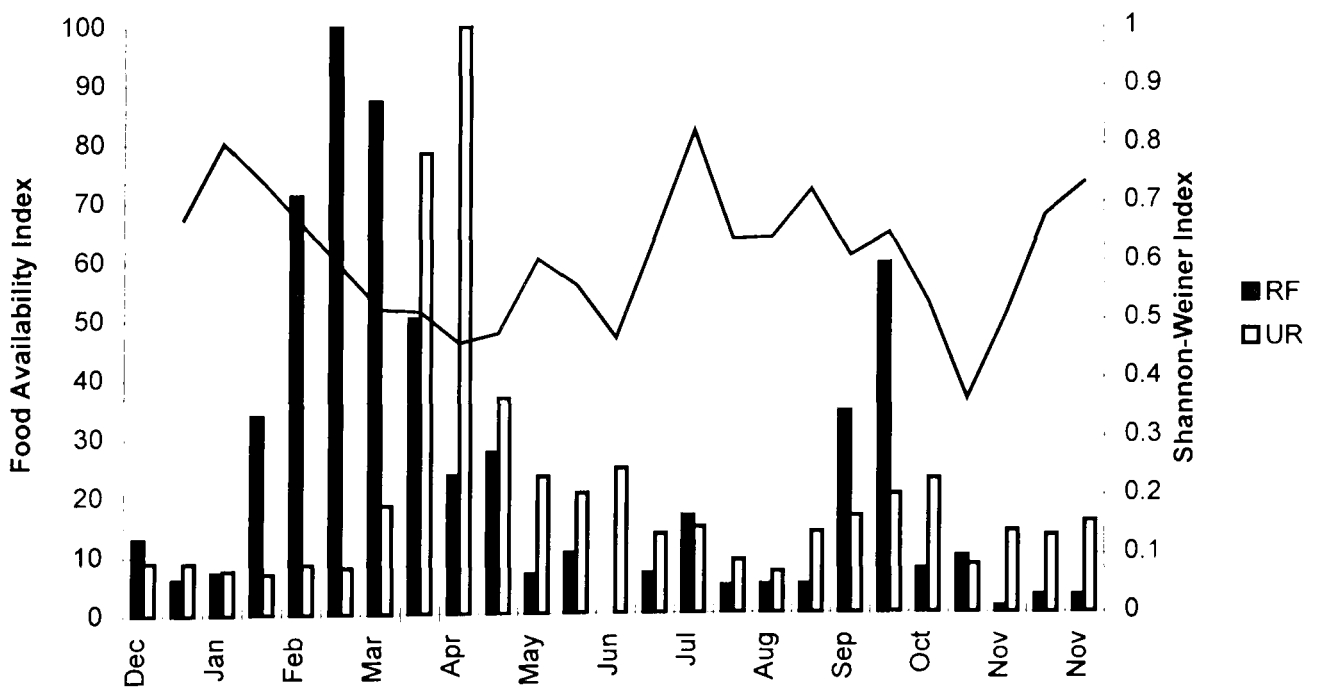
Table 6.3 List Of Species Which Account For >0.5% Feeding Time.

Species	%Feeding Time
Ficus sur	25.841
Broussonetia papyrifera	19.873
Ficus mucuso	15.962
Cynometra alexandrii	10.425
Celtis mildbraedii	7.276
Ficus exasperata	4.216
Mildbraediodendron excelsum	2.121
Urera camaroonensis	1.575
Ficus variifolia	1.270
Ficus barteri	1.143
Ficus sansibarica	1.117
Celtis zenkeri	0.902
Celtis wightii	0.863
Morus lactea	0.825
Alafia	0.800
Desplatia dewevrei	0.571
Total	94.78

Seasonal Changes in Diet

The mean number of plant species observed to be eaten by the chimpanzees per two week phenology period was 8.48 (+/-0.567 S.E.) The number of food species eaten during each phenological period was significantly and positively correlated to measures of food availability (young leaves r_s =0.502, $p<0.01$; and the combined measure of all food availability r_s =0.413, $p<0.05$). This suggests that during periods of high food availability the chimpanzees increase dietary diversity. However, *Shannon-Wiener i*ndices did not support this suggestion. The standardised Shannon-Wiener index (J'), is a more sensitive measure of dietary diversity than simple counts of the number of species in the diet as it also accounts for the relative *proportion* of each species in the diet. The mean degree of diversity across all phenology periods was 0.61 (+/-0.02 S.E.). These indices were significantly and *negatively* correlated with the availability of ripe fruit (r_s = -0.448, $p<0.05$) and unripe fruit (r_s = -0.409, $p<0.05$). The Shannon-Wiener indices were also significantly and negatively correlated with the amount of time spent foraging (r_s = -0.443, $p<0.05$) and positively correlated with the proportion of time spent moving (r_s =0.441, $p<0.05$) and the time spent feeding on young leaves (r_s =0.476, $p<0.05$).

Fig 6.4 Temporal Variation In The Standardised Shannon-Wiener Index, Shown As A Moving Average (Line) And The Food Availability Index Of Ripe And Unripe Fruit (Bars) Along The Phenology Trail.



Thus, dietary diversity seems to increase as a response to food, in particular fruit, scarcity. This is suggested by the negative correlation between the Shannon-Wiener diversity indices and phenology variables and also confirmed by the relationship between the standardised Shannon-Wiener indices and the activity budgets and feeding behaviour data.

Table 6.4 Count Of Species In Diet During Each Phenological Period And The Corresponding Standardised Shannon-Wiener Indices.

Phenology Period	No. Species	J'
Dec(3)	7	0.523
Jan(1)	10	0.823
Jan(2)	7	0.781
Feb(1)	13	0.693
Feb(2)	10	0.635
Mar(1)	13	0.546
Mar(2)	7	0.491
Apr(1)	9	0.538
Apr(2)	9	0.384
May(1)	13	0.571
May(2)	12	0.637
Jun(1)	3	0.481
Jun(2)	10	0.457
Jun(3)	3	0.830
Jul(1)	8	0.817
Jul(2)	4	0.459
Aug(1)	7	0.822
Aug(2)	11	0.623
Sep(1)	7	0.596
Sep(2)	11	0.702
Oct(1)	8	0.357
Oct(2)	8	0.371
Nov(1)	8	0.649
Nov(2)	6	0.708
Nov(3)	8	0.757

To determine which were the most preferred species of food, a *rank preference index* for the principal food species (Table 6.3), which were also monitored along the phenology trail, was calculated (Table 6.5). *Celtis wightii*, (CWI) was not monitored along the phenology trail, therefore for the purposes of constructing the rank preference index the availability of the related species, *Celtis mildbraedii*, (CMI)was used to predict the preference of *C. wightii*.

Table 6.5 The Rank Preference Of The Principal Food Species.

Food Species	Rank
Ficus mucuso	-3.46
Celtis mildbraedii	-2.16
Ficus sur	-1.662
Mildbraediodendron excelsum	-1.04
Broussonetia papyrifera	-0.460
Cynometra alexandrii	0.06
Ficus exasperata	1.04
Ficus varifolia	2.02
Celtis wightii	2.52
Ficus sansibarica	3.02
Celtis zenkeri	3.76
Morus lactea	8.82

The results show that two of the species which account for the majority of feeding time are also highly preferred species (*F. mucuso* and *F.sur*). The rank preference index also highlights the importance of the young leaves of *C. mildbraedii* in the diet.

Food availability ranks were determined for the overall availability of young leaves, buds, flowers and fruits so they do not distinguish food items, but the table of food items shows (Table 6.2) that it is the flowers and leaves of this species which the chimpanzees feed upon. Observation showed that young leaves were the primary food item from *Celtis mildbraedii*. So, this suggests that the young leaves of *Celtis mildbraedii* are selected over the availability of other fruiting species.

Figures 6.5 & 6.6 show the selection of different food species in the diet and the overall food availability measures for each species. The figures are drawn for all the species included in the rank preference analyses. These figures show the inclusion of a particular species in the diet is not always a direct reflection of the availability of that species.

Fig 6.5 Charts Of The Availability Of Ripe Fruit Along the Chimpanzee Food Species Phenology Trail (Bars) And The Proportion Of Feeding Time Spent On Each Species (Lines).

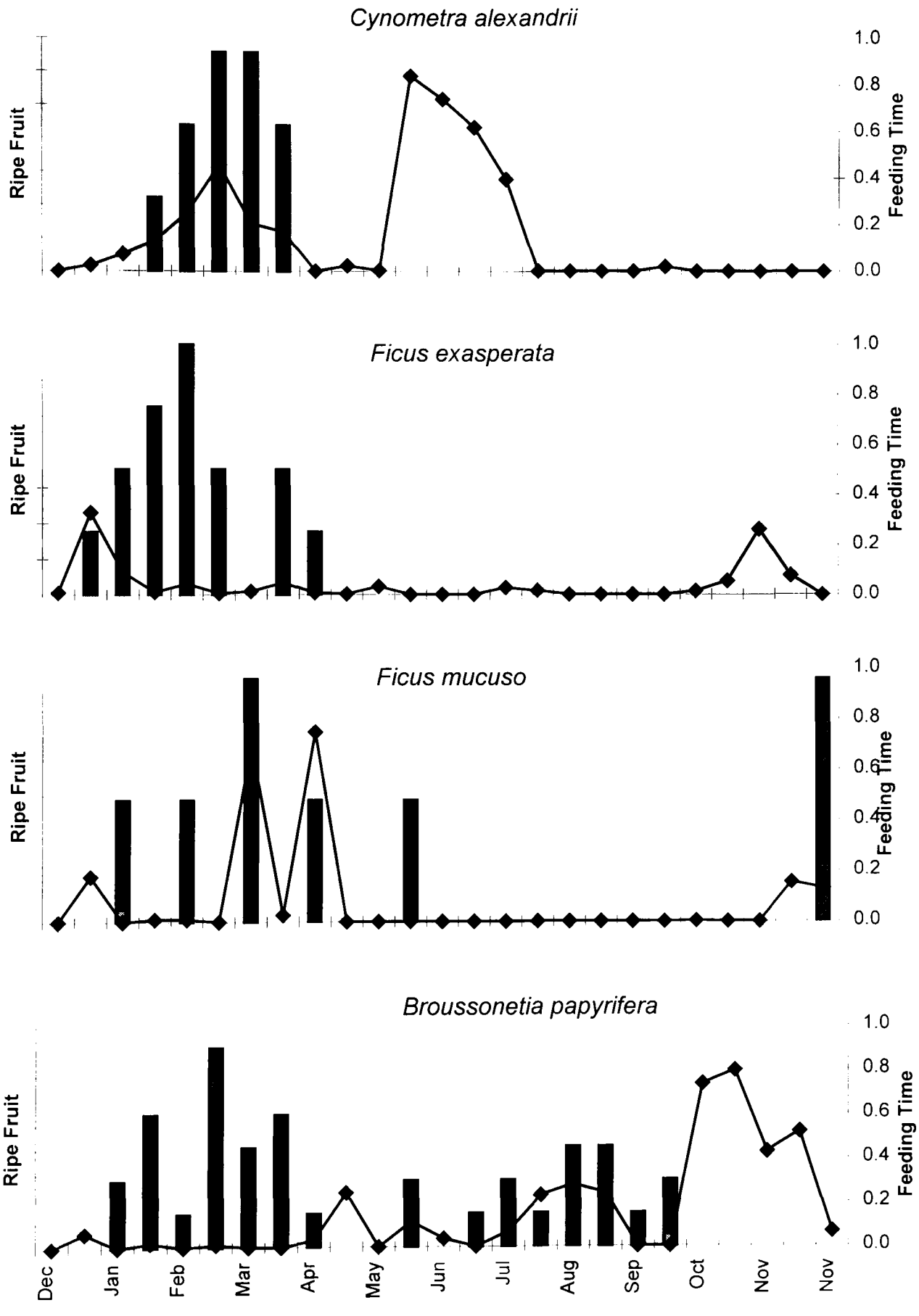


Fig 6.5 continued.

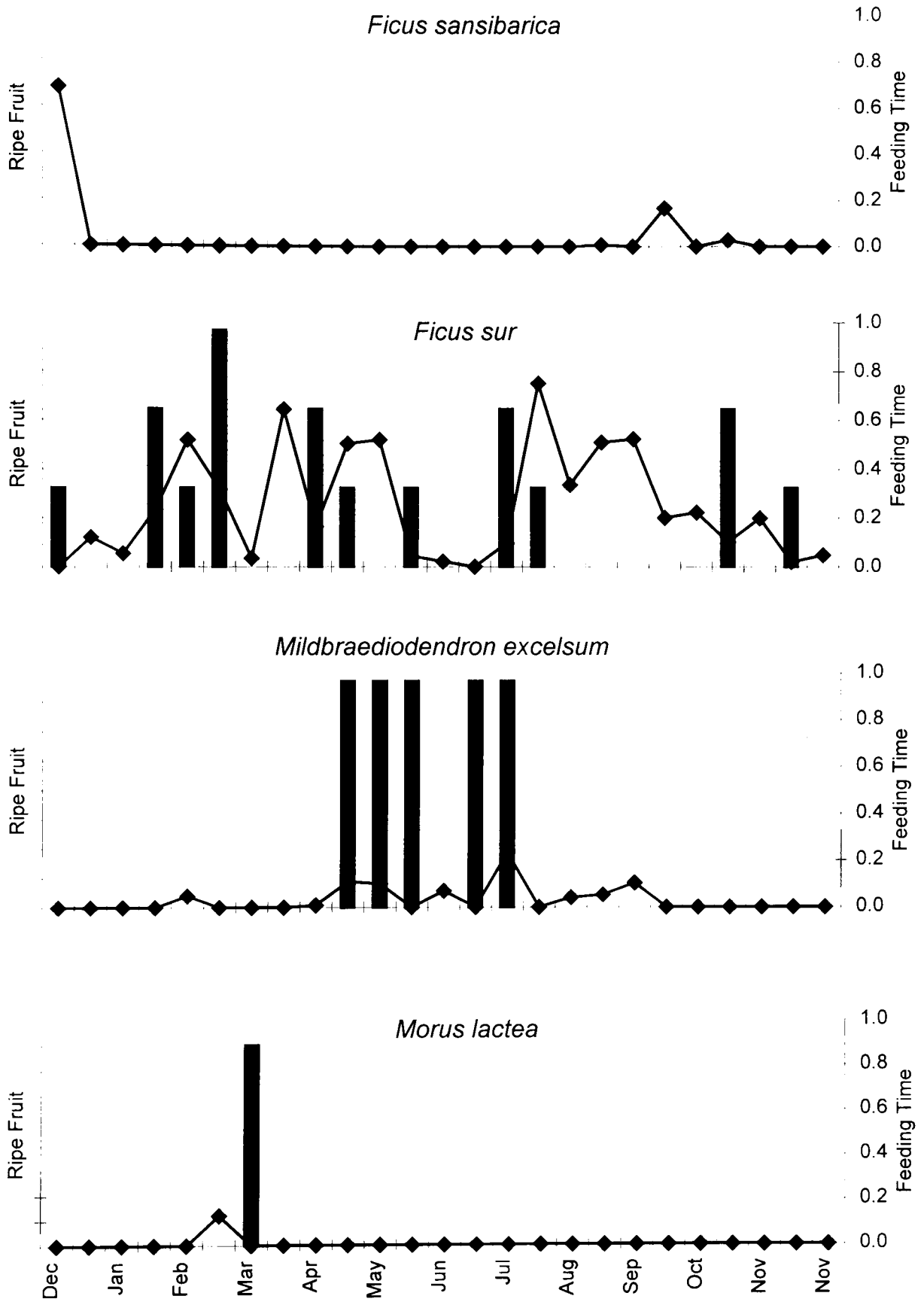
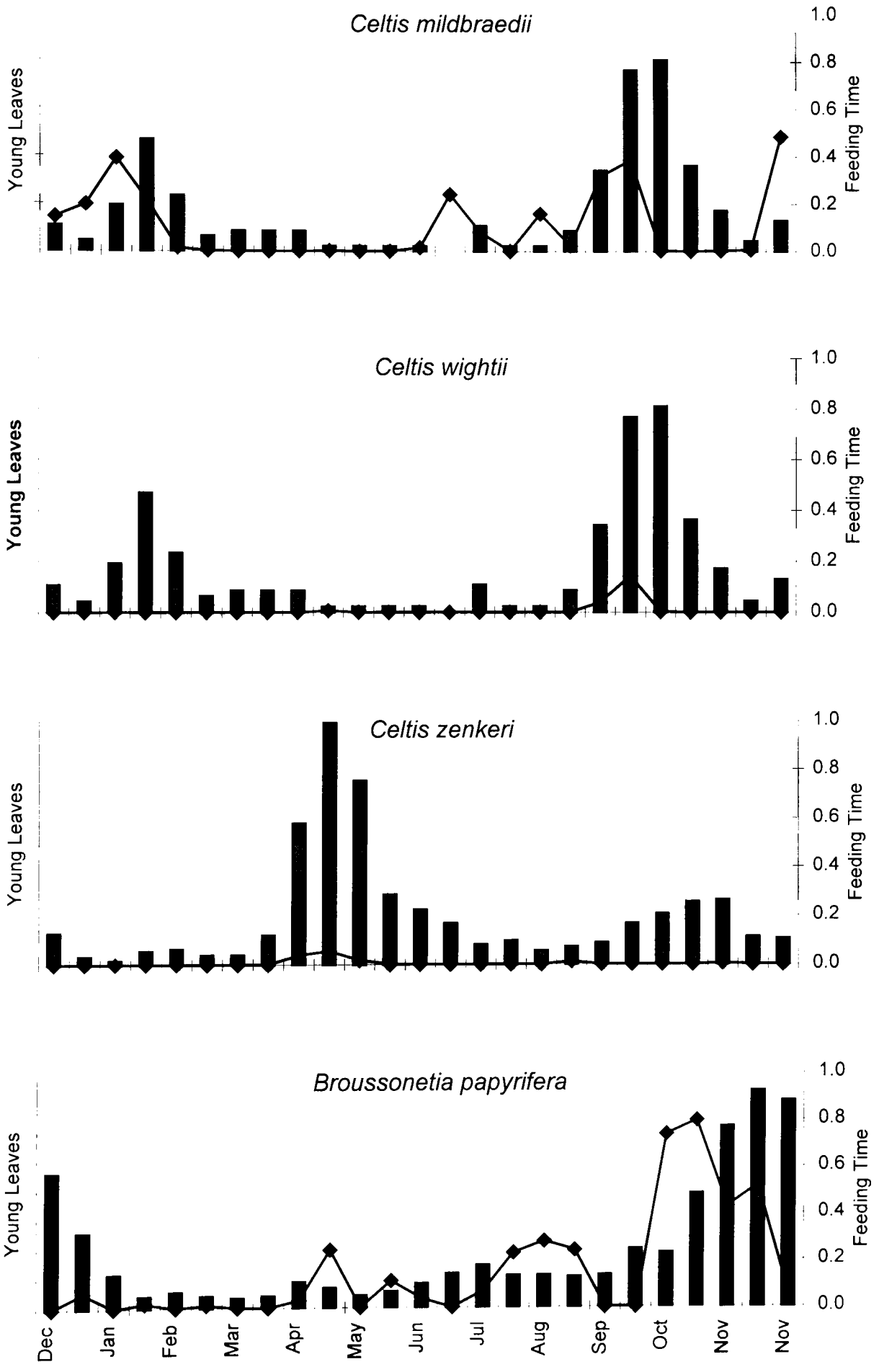


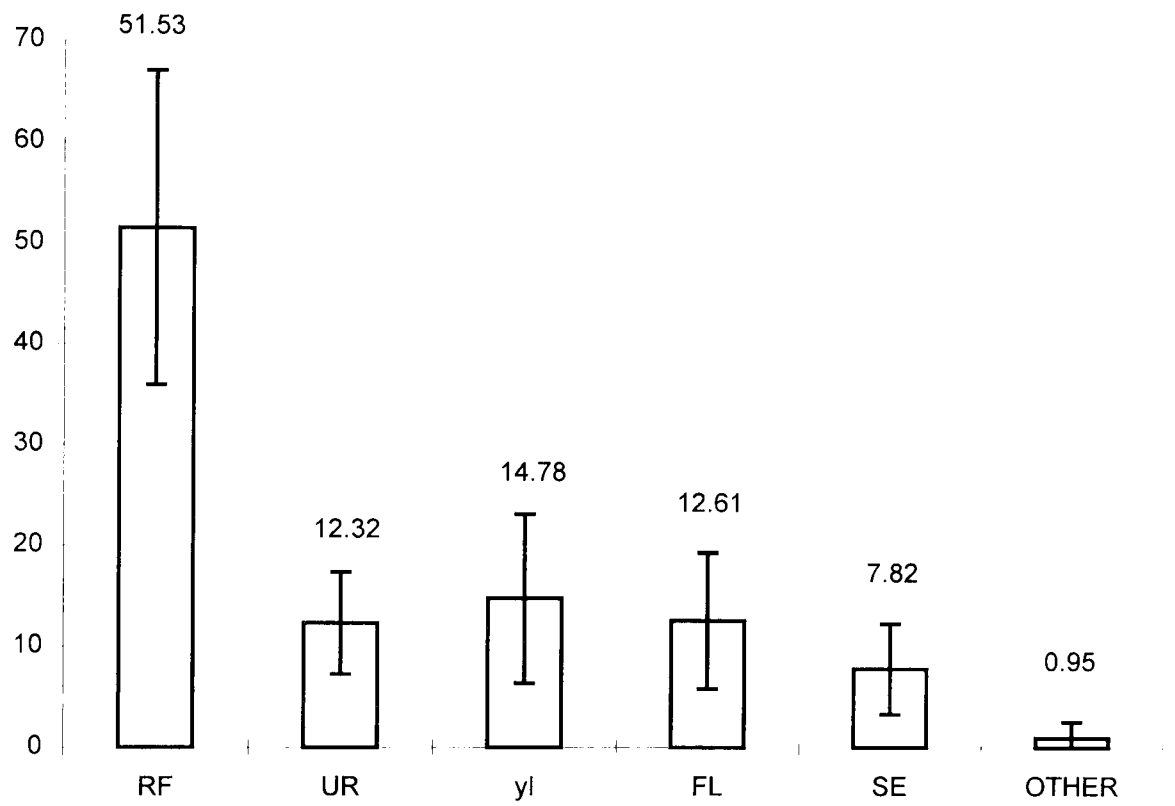
Fig 6.6 Charts Of Availability Of Young Leaves (Bars) And The Proportion Of Feeding Time Spent On Each Species (Lines).



Percentage Time Spent Feeding on Different Food Items

The majority of feeding time was spent feeding on fruit (63.8%), and 80.72% of this time was spent on ripe fruit (see Fig 6.7).

Fig 6.7 Percentage Of Feeding Time Spent Feeding On Different Food Items (RF = ripe fruit, UR = unripe fruit, YL = young leaves, FL = flowers, SE = seeds, Other = combined values of unknown food item, bark, pith, and rotten wood.)



Sex and life history differences in the percentage of different food items in the diet were investigated. Mann-Whitney tests were used to investigate the differences between all-males and all-females, adult males and adolescent males, adult females and adolescent females, cycling and non-cycling females. Females were found to spend significantly more time feeding on ripe fruit than males, ($W= 230$, $p<0.01$ Table 6.6) and unripe fruit ($W=396$, $p<0.01$ Table 6.6). There was also a significant sex difference for the time spent feeding on young leaves, with males found to spend more time feeding on leaves than females ($W=269$, $p<0.01$). In addition, cycling females were found to spend a significantly greater amount of time feeding on unripe fruit than non-cycling females ($W=70$, $p<0.05$).

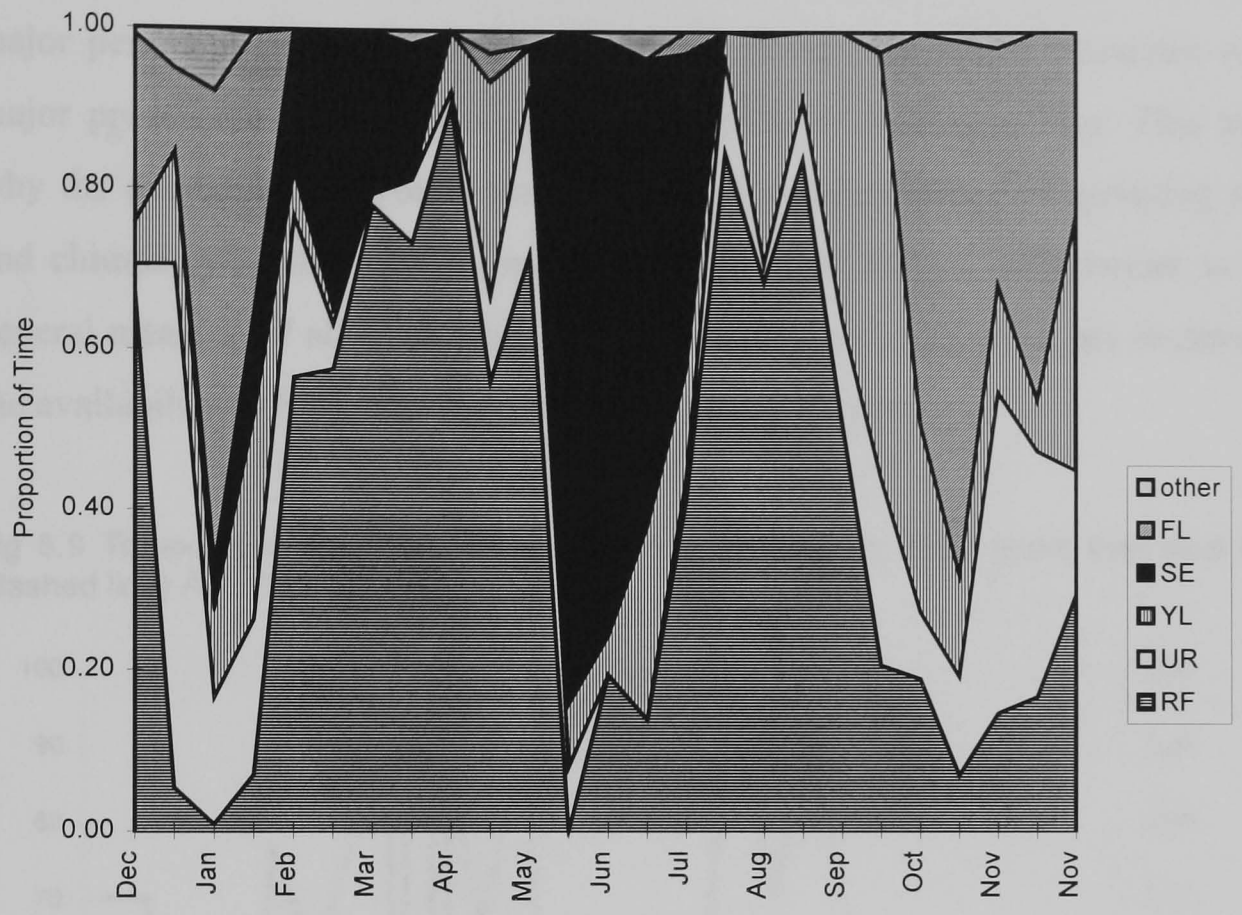
Table 6.6 Mean Percentage Of Time Spent Feeding On Different Food Items For Each Age And Life History Class And Standard Error.(RF = ripe fruit, UR = unripe fruit, YL = young leaves, FL = flowers, SE = seed.)

	N	RF	UR	YL	FL	SE	Other
All-Males	**17**	**44.0**	**14.8**	**17.5**	**13.3**	**9.2**	**1.2**
st. err.		*1.7*	*0.9*	*1.3*	*0.9*	*0.9*	*0.3*
All-Females	**19**	**55.7**	**10.8**	**13.1**	**12.6**	**7.0**	**0.8**
st. err.		*3.5*	*1.1*	*1.6*	*1.9*	*1.1*	*0.2*
Adult Males	**12**	**45.0**	**14.8**	**16.6**	**12.7**	**10.0**	**0.9**
st. err.		*1.8*	*1.2*	*1.6*	*1.1*	*1.2*	*.0.2*
Adult Females	**12**	**59.3**	**8.9**	**11.3**	**12.1**	**7.6**	**0.8**
st. err.		*3.4*	*1.2*	*1.4*	*2.7*	*1.5*	*0.3*
Adolescent Males	**4**	**40.8**	**15.5**	**19.9**	**14.5**	**7.0**	**2.2**
st. err.		*5.4*	*1.1*	*2.9*	*2.1*	*1.4*	*1.1*
Adolescent Females	**6**	**53.7**	**12.8**	**14.3**	**12.7**	**5.6**	**0.9**
st. err.		*7.3*	*1.1*	*3.3*	*2.9*	*1.3*	*0.4*
Cycling Females	**8**	**50.9**	**12.7**	**16.7**	**12.1**	**6.8**	**0.9**
st. err.		*3.0*	*1.2*	*1.4*	*2.2*	*1.5*	*0.3*
Non-Cycling Females	**10**	**62.7**	**8.2**	**8.8**	**12.5**	**7.0**	**0.7**
st. err.		*4.9*	*1.1*	*1.7*	*3.3*	*1.7*	*0.4*

Seasonal Variation of Food Items in Diet.

There was variation between months in the proportion of different food items included in the diet (see Fig 6.8). The proportion of time spent feeding on ripe fruit was significantly and negatively correlated with the proportion of time spent feeding on young leaves (r_s = -0.414, $p<0.05$) and flowers (r_s = -0.601, $p<0.001$). The proportions of time spent feeding on young leaves and bark were significantly and positively correlated (r_s =0.434, $p<0.05$). The proportion of THV in the diet was significantly and positively correlated with the proportion of seeds (r_s =0.419, $p<0.05$) and the proportion of seeds in the diet was negatively correlated with the proportions of unripe fruit (r_s = -0.414, $p<0.05$) and young leaves (r_s = -0.401, $p<0.05$).

Fig 6.8 Proportion of time spent feeding on different food items throughout the year by the independent individuals of the Sonso community; FL= flowers; YL= young leaves; SE= seeds; UR= unripe fruit; RF= ripe fruit.



There are no significant correlations between the proportion of time spent feeding on a given food item and the availability of that food item. This suggests that the decision to feed upon food items is not solely based upon availability. It appears that despite fluctuations in the availability of ripe fruit the chimpanzees are able to maintain a high proportion of ripe fruit in the diet. There are three periods when ripe fruit is not the single major component of the diet. These occur during January and October at which times the major component of the diet is flowers (see Fig 6.9) and between June and July when the major component is the seeds of *Cynometra* (see Fig 6.8). The period between June and July was the time of major food scarcity during the study period. During this time the chimpanzees were observed to move out of the usual community range area and feed on the seeds of *Cynometra* and the fruit of *Mildbraediodendron* It was at this time that there was an overlap of the Sonso community range with that of another community.

Examination of the patterns of the proportion of diet that is fruit and young leaves shows that the proportion of young leaves in the diet peaks during the second period of production in September and October (see Fig 6.10). However, during the major period of production at the beginning of the year which coincides with the major production of fruit, leaves were not eaten in large quantities. This suggests why the availability of young leaves is such a good predictor of grouping patterns and chimpanzee behaviour in general. It also shows why it is important to have a general measure of all food availability, because the chimpanzees are responding to the availability of fruit, leaves and flowers during the year.

Fig 6.9 Temporal Variation In The Time Spent Feeding On Fruit (solid line) And Flowers (dashed line) And Fruit Availability (bars).

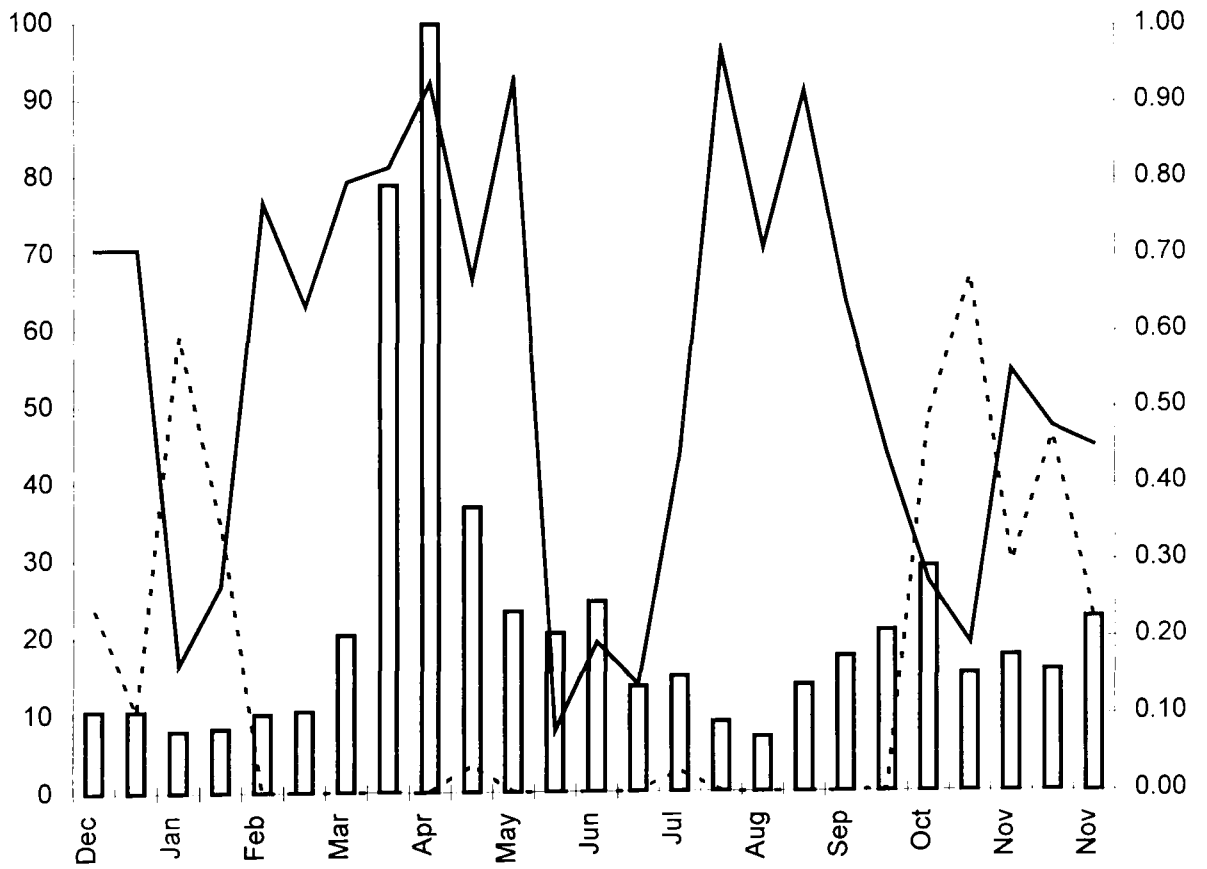
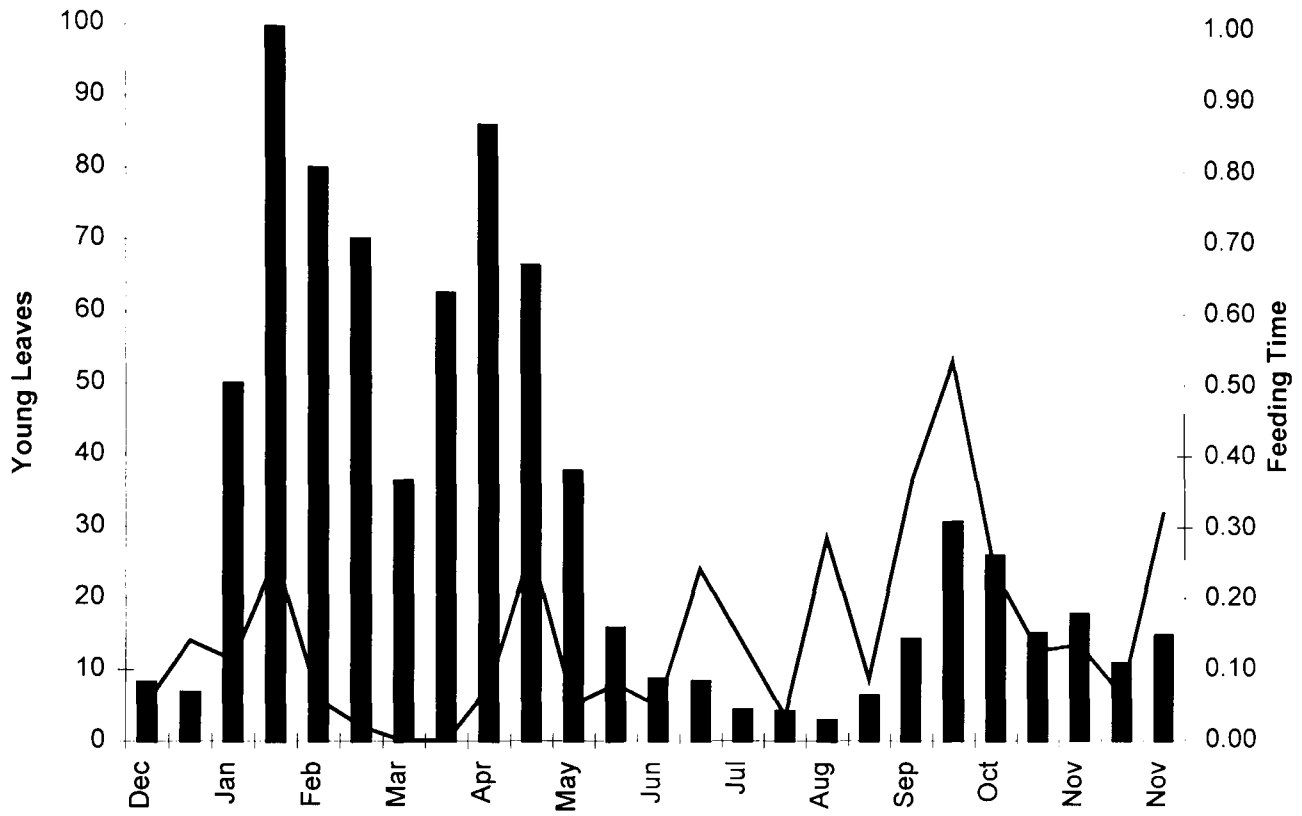


Fig 6.10 Temporal Variation In The Availability Of Young Leaves Along The Phenology Trail (bars) And The Proportion Of Time Spent Feeding On Young Leaves (line).



Faecal Analyses of Diet

A total of 161 faecal samples were collected between January and November 1998. A total of 59 food items were recorded in them; fruit spp.(seed + flesh) = 40 (66.66%); leaf spp.=5(8.33%); pith (1.6%); other =14 (23.33%). Pith could not be identified to species. The term 'seeds' used with reference to dung analyses, refers to the seeds of edible fruit species and is therefore an indicator of the proportion of fleshy fruit eaten.

Table 6.7 List Of Food Items Found In Dung Samples (In Alphabetical Order); Numbers Represent Number Of Faecal Samples Containing Food Item.

		SE	FL	YL	ML	BK	Other
Anacardiaceae	Pseudospondias microcarpa	1					
Apocynaceae	Alafia sp.	26	22				
Boraginaceae	Cordia millenii	8	11			1	
Cecropiaceae	Myrianthus holstii	20	2				
Commelinaceae	Commelina spp.			2 (whole)			
Flacourtiaceae	Calconcoba schweinfurthii		2				
Leguminosae	Cynometra alexandrii	20				4	
	Dialium excelsum	23	5				
Meliaceae	Khaya anthotheca					2	3 (resin)
Moraceae	Antiaris toxicaria	6	1				
	Broussonetia papyrifera	21					
Moraceae	Ficus exasperata	6					
	Ficus spp.	68					
	Ficus mucuso	9					
	Ficus sansibarica	10					
	Ficus sur	62					
	Morus lactea	4					
Sapotaceae	Chrysophyllum albidum		1				
	Chrysophyllum gorungosanum	3					
Ulmaceae	Celtis mildbraedii			42			
	Celtis wightii			2			
Urticaceae	Urera camaroonensis	83					
Zingiberaceae	Aframomum spp.	2					
	Unidentified spp.			28 (1whole)	1	7	4
	Caterpillar (unknown spp)						31
	Chimp hair						19
	Invertebrate spp						4
	Lichen						1
	Root						1
	Soil						34

Table 6.8 Mean Number Of Species Per Food Item Category And The Mean Proportion Of Each Category Per Dung Sample.

	Number of Species	*Std Err.*	Percentage of sample	*Std Err.*
Flesh	0.881	*0.052*	18.173	*1.527*
Leaf	0.553	*0.043*	19.125	*2.045*
Other (food)	0.609	*0.056*	1.889	*0.529*
Pith	0.677	*0.037*	4.637	*0.701*
Seed	2.832	*0.089*	56.174	*2.102*
Total Fruit	2.776	*0.093*	74.348	*2.365*

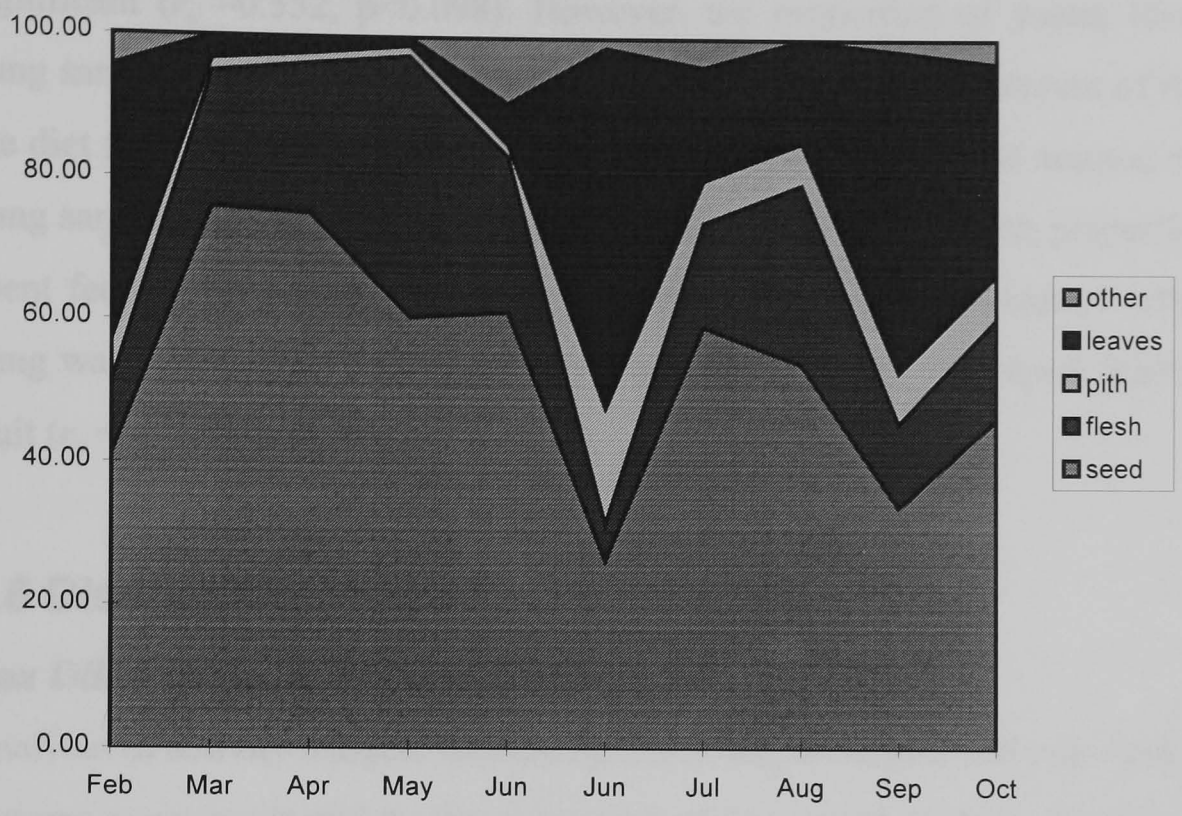
When all samples are considered fruit is the major food both in terms of number of species eaten and in terms of abundance in the diet.

Due to the small number of dung samples collected during some of the phenology periods, adjacent two week periods were combined resulting in a total of 10 different sub-samples and phenology periods (see Table 6.9). These samples were then analysed for correlations between different food items. The proportion of all fruit in the dung samples (flesh and seeds) was significantly and negatively correlated with proportion of young leaves(r_s = -1.000, p<0.000) and pith (r_s = -0.9030, p<0.000). In addition the proportion of leaves in dung samples was significantly and positively correlated with the proportion of pith (r_s =0.903, p<0.000) and negatively with the proportion of seeds (r_s = -0.903, p<0.0001). The proportion of pith was also negatively correlated with the proportion of seeds (r_s = -0.830, p<0.01). The proportion of flesh in the dung samples was negatively correlated with the number of species in the dung samples (r_s = -0.685, p<0.05)

Seasonal Variation

The only significant correlation between the proportion of food items represented in dung samples and measures of food availability was a negative one between the proportion of pith and the availability of young leaves (r_s = -0.673, p<0.5), which as stated previously is probably also an accurate reflection of overall food availability. Therefore, the analysis of diet using dung was useful. It highlighted that pith is eaten by the Sonso community, albeit at low levels, and that the proportion of pith in the diet increased when general food availability was low, suggesting its use as a fall-back food.

Fig 6.11 Temporal Variation In The Proportion Of Different Food Items In Faecal Samples



Feeding Observations Compared To Faecal Data

There was no significant correlation between the mean number of species found in the dung samples during each phenological period and the number of species observed to be fed upon during the same time period (See Table 6.9).

Table 6.9 The Mean Number Of Species Of Food Represented In The Dung Samples Per Phenological Period And The Corresponding Number Of Food Items Observed To Be Fed Upon.

Month	No. dung samples	No. Species Dung	No. Species Observed
Feb	17	5.043	10
Mar	29	4.718	11.5
Apr	19	5.060	8
May	16	3.600	11
Jun	6	4.333	7.5
Jun	7	5.750	6.5
Jul	16	5.400	6
Aug	11	2.636	9
Sep	17	4.803	9
Oct	17	4.010	8

The percentage of time spent feeding on fruit during each month was significantly and positively correlated with the total percentage of fruit in the dung samples (r_s =0.709, $p<0.05$). There was a positive correlation between the time spent feeding on

young leaves and the proportion of young leaves in the dung however this was not significant (r_s =0.552, p<0.098). However, the proportion of young leaves in the dung samples was significantly negatively correlated with the amount of ripe fruit in the diet from feeding observations (r_s = -0.709, p<0.05), and the amount of seeds in dung samples was significantly and negatively correlated with the proportion of time spent feeding on young leaves (r_s = -0.746, p<0.01). The amount of 'other' in the dung was significantly and negatively correlated with the time spent feeding on ripe fruit (r_s = -0.650, p<0.05).

6.6 Discussion

Sex Differences in Activity Budget and Diet

Analyses of activity budgets showed that both overall annual and two weekly activity patterns were dominated by the proportion of time spent feeding. However, due to a methodological bias towards feeding parties (see General Methodology chapter), time spent travelling on the ground and other terrestrial activities may be under-represented. Males were found to spend significantly more time moving than females, but this also should be viewed with caution given the greater ease of following male individuals on the ground due to greater levels of habituation, and also the tendency for males to travel in larger, and thus easier to follow, parties. However, among females, there were significant differences in the time spent moving dependent on reproductive state. Cycling females were found to spend significantly more time moving and socialising than non-cycling females. There was a non-significant trend for cycling females to compensate the extra time spent moving by spending less time foraging than non-cycling females. This suggests that there is a cost to oestrous. These data, together with the ranging data (Chapter 7), suggest that females leave their core areas when in oestrus, presumably to increase the likelihood of encountering potential mates. Wrangham (1979b) and Hasegawa (1990) both found that cycling females travelled further than non-cycling females. The only other study to investigate changes in activity patterns between cycling and non-cycling females also found that cycling females spent significantly more time moving than non-cycling females (Matsumoto-Oda & Oda, 1998a). The increase in time spent

moving was not significantly correlated with any other behavioural category. but four of the five females studied showed a reduction in time spent feeding. Matsumoto-Oda & Oda, 1998a) compared the activity patterns of individual cycling females when exhibiting and not exhibiting a full sexual swelling. The present study classifies females as either exhibiting full sexual swellings during the study or not. This reduces sources of bias from sampling females during times of different food availability. Ghiglieri (1984) found that males spent significantly more time feeding and travelling and less time resting compared to females, but his study also experienced biases introduced by partial habituation of the chimpanzees. Other studies have found no significant differences between the sexes in activity patterns, although few distinguished cycling and non-cycling females. Doran (1997) found no sex differences in the time spent feeding, moving and resting. Wrangham & Smuts (1980) found no sex differences in the time spent feeding, and Hunt (1989 cited in Doran 1997) found no sex differences in the time spent in locomotion.

Sex differences in diet showed that, overall, males spent significantly less time feeding on ripe fruit than females and more time feeding on unripe fruit. Within females, cycling females were found to spend a greater proportion of time feeding on unripe fruits. Chimpanzees spent more time feeding on ripe than unripe fruit, suggesting a preference for ripe fruit. The fact that both males and cycling females spent significantly more time feeding on unripe fruit suggests a possible cost to associating in larger groups may reduced proportion of ripe fruit in the diet. Strangely, males were observed to spend a greater proportion of time feeding on young leaves than females, thus having a higher in take of protein. Lactating females are usually thought to have increased protein demands, so I would have expected that if there was an observed difference between the sexes, females would have spent more time feeding on young leaves.

Response to Food Scarcity.

There were no consistent relationships between the proportion of a particular food item in the diet and phenological measures. This suggests that chimpanzees are

meeting their metabolic demands through various different combinations of food items throughout the year.

Considering the whole community, the proportion of time spent feeding was significantly and positively correlated with the availability of young leaves and the combined food availability measure of all food items. As mentioned in the results section, the pattern of availability of young leaves is similar to the combined measure of food availability. In addition, the time spent resting and grooming were inversely correlated to the same measures of food availability. This indicates that the chimpanzees are responding to a decrease in food availability by decreasing the time spent foraging and increasing the time spent resting and grooming. However, although this may be the case in general throughout the course of the year, detailed examination of the chart of seasonal changes in activity patterns shows a different response during the most severe period of food scarcity. During the month of July, there was a dramatic increase in the time spent moving and a corresponding decrease in the time spent feeding and resting. The feeding data show that during this time *Cynometra* seeds were the most important food item in the diet. Seeds contain all the nutrients required for a seedling during germination and therefore may be a complete food resource for primates and thus a good key-stone food in times of food scarcity. However, during this time the *Cynometra* trees within the study community's core area were not bearing seeds. It was at this time that the chimpanzees were commonly seen in the nature reserve, and the community home range overlapped that of the neighbouring community. It would certainly appear that the chimpanzees were travelling long distances in order to feed on the seeds of *Cynometra* and also *M. excelsum*, which was also fruiting in this area. Therefore the results suggest that the Sonso chimpanzees have a flexible strategy in response to periods of food scarcity. Generally, when food scarcity is not severe they appear to decrease time spent feeding and increase the proportion of time spent resting, thus conserving energy. However, there is also evidence to suggest that in times of extreme food shortage the chimpanzees will change their ranging patterns in order to maintain a diet of fruit and some seeds. This is in contrast to the results from the Tai community, where during periods of food scarcity the chimpanzees spent more time feeding. At Tai the time

spent feeding on young leaves was greatest in the minor dry season of July and August, also the time of least percentage of fruit in the diet (Doran, 1997). It is important to note that the major period of food scarcity in Budongo Forest is a period of scarcity of both fruit and young leaves, thus perhaps young leaves were not an option for use as a keystone food at this time. Data from faecal samples largely support this argument. The proportion of fruit in each sampling period was positively correlated with the availability of ripe fruit whereas the proportion of young leaves was negatively correlated with ripe fruit. The faecal data also showed an increase in the utilisation of THV during periods of food scarcity. These results appear to be similar to the responses of chimpanzees at Lopé (Tutin et al. 1991; Tutin & Fernandez, 1993b), where, when succulent fruits are scarce, the chimpanzees increase their consumption of vegetative foods and also rely on the fruit of the oil palm, *Elaeis guineensis*. When succulent fruit was scarce for longer periods of time, then the chimpanzees at Lopé fed on wind- and mechanically-dispersed seeds of trees of the families *Caesalpiniaceae* and *Papilioniaceae*, if available. In addition, young leaves were incorporated into the diet according to availability. THV has also been reported to be an important keystone resource at Kibale (Wrangham et al., 1991, 1996) and for bonobos (Kano, 1992; Malenky et al., 1994). At Lomako, the bonobo diet showed no consistent seasonal variations in the dietary breadth or use of THV, fruit and young leaves (White, 1998). It has been suggested that seasonality at Lomako is less marked than at other chimpanzee sites and that although group size varied with food availability because there was no period of extreme food shortage, females were able to maintain social cohesion throughout the year (White, 1998).

The Shannon-Wiener indices of dietary diversity were negatively correlated with the availability of ripe and unripe fruit and the time spent foraging, indicating that in accordance with the theory of optimal foraging when fruit availability is high, the Sonso chimpanzees concentrated their feeding time on one or two food species. In addition, the Shannon-Wiener indices were positively correlated with time spent moving, indicating that an increase in dietary diversity is associated with increased searching for food. Interestingly, the number of species included in the diet increased with increasing food availability. This measure of dietary diversity however, does not

consider the proportion of time spent feeding on each species. It is possible that during the periods of high food availability the chimpanzees are experimenting on novel food species or feeding opportunistically on other fruiting species. Wrangham (1977) suggested that chimpanzees will include a small proportion of certain food items as if testing to see their value as a food resource. Due to the extreme variability between years in the availability of some foods, chimpanzees need to be able to feed upon a wide range of food items. As stated by Tutin et al. (1991), it may be as a result of the constant search for new food resources that chimpanzees have adopted tool use to extract food. Three species which were important food items during Newton-Fisher's (1999b) study were not seen to be eaten during this study. The field assistants noted that the species *Celtis durandi* and *Maesopsis eminii* had not produced the same abundant fruit crop as in previous years. This pattern of inter-annual variation in both fruit production and crop size has been reported from other sites (Tutin & White, 1998).

As a family, the Moraceae is particularly important in the diet of the Sonso chimpanzees. The top three species by percentage time spent feeding are all in this family. Comparison with similar data from Newton-Fisher (1999b) show this choice to be consistent between years. Interestingly, Broussonettia papyrifera is an exotic species and although not highly preferred, is important in the diet of the chimpanzees. The chimpanzees feed on the young leaves, fruit and flowers of this species. The rank preference index showed that chimpanzees were strongly selecting for the fruits of fig species. Fig species may be regarded as a keystone food for chimpanzees in Kibale (Wrangham et al., 1996), but it is obvious that in Budongo the chimpanzees are choosing to feed on certain species of figs even in preference to other fruit species. Overall nutritional analyses of eaten and non-eaten foods suggested that the chimpanzees were selecting foods based upon sugar levels and were not avoiding tannins (Reynolds et al., 1998). Similar conclusions were made by Nishida (2000) based on food taste. Reynolds et al. (1998) suggested that the wadging behaviour in chimpanzees may reduce tannin intake and perhaps also the chimpanzees produce salivary muco-proteins which bind to tannins. Nutritional analyses of nine species of fig at Kibale Forest and comparison with *Mimusops*

bagshawei, the most common non-fig food in the chimpanzee diet showed that the nutritional content of fig pulp was similar between figs and non-fig food (Wrangham et al., 1993). The only difference was that fig food had a lower concentration of sugars. In addition, the chimpanzees were found to prefer large fruits and large fruit patches (Wrangham et al., 1993). In this study the chimpanzees showed greatest preference for *Ficus mucuso*. Both the fruits and the canopy of mature trees of this species are relatively large. Thus, individuals may form large parties and maximise patch residence time. The chimpanzees were observed to wadge the fruit of *F. mucuso*, (as well as other species), thus probably avoiding the higher condensed tannin, lipids and fibre content of the seeds (Wrangham et al. 1993). In addition, analysis of figs from 3 continents have shown figs to have a significantly higher content of calcium than other fruits (O'Brien et al., 1998). Thus, figs may be important as a keystone food by providing an adequate balance of calcium among frugivores. Interestingly, *Celtis mildbraedii* was also a highly sought-after species. It was only the leaves of this species which were fed upon, suggesting that although the chimpanzees are categorised as frugivorous, young leaves are an important food. Kuroda et al. (1996) also noted that *C. mildbraedii* was an important food species for the chimpanzees in Ndoki forest in northern Congo. It was the only food species whose young leaves were fed upon by both chimpanzees and gorillas, the rest being exclusively fed upon by gorillas. This suggests that *C. mildbraedii* young leaves may lack toxins. Reynolds et al. (1998) analysed the sugar and tannin content of eaten and non-eaten parts of *C. mildbraedii* and *B. papyrifera* leaves together. Although the sample size of mature leaves was small, no differences in the tannin content between young and mature leaves were found, however there was a significantly greater concentration of glucose in young leaves. Sonso chimpanzees were observed to feed upon *C. mildbraedii* intensively when available during the lesser fruiting season. At Ndoki, *C. mildbraedi*i is one of the most dominant species in the mixed-species forest, and most canopies could support at least 10 apes. At Budongo, it is an abundant tree species and some trees have very large canopies capable of supporting large chimpanzee groups, but chimpanzees also fed in smaller trees, even those that could support only one individual. These were abundant in the mixed forest type.

However, although individual trees were small, their high density allowed chimpanzees to remain in association with each other, even when in separate trees. In general, the time spent feeding on ripe fruit was negatively correlated with the time spent feeding on young leaves, suggesting the use of these items as keystone resources. However, the data also suggest that *C. mildbraedii* leaves were highly preferred food items at other times. Further supporting the idea that young leaves may be used as a keystone resource, the proportion of bark in the diet was positively correlated with that of young leaves. Bark has been described as a seasonal food resource for gorillas (Rogers et al., 1994). In addition, the proportions of THV and seeds in the diet were positively correlated, confirming their use as keystone foods. However, the proportion of seeds in the diet was negatively correlated with the proportions of unripe fruit and young leaves. This suggests that if both seeds and young leaves are used as keystone resources they are used during different time periods.

Chimpanzees as Seed Dispersers and Seed Predators.

Generally, chimpanzees may be considered as seed dispersers. The intact seeds of 17 species were found in dung samples. Further data are required on germination and seedling survival in order to assess the efficacy of chimpanzees as seed dispersers.

Chimpanzees may be considered as seed predators of *Cynometra*. This tree species produces its seeds in pods, designed for wind dispersal. Typical species that use aerial mechanisms to disperse their seeds produce copious amounts of seeds, in comparison to fleshy fruits which typically invest a lot of energy in a single fruit. Therefore the cost to *Cynometra* individuals of the seeds being eaten by the chimpanzees may be negligible. The seeds produced by *Cynometra* are very large and surrounded by a tough seed coat which offers some protection from potential consumers. The chimpanzees, however, possess the physical power and cognitive abilities to open the seed pods and feed on the seeds before they are dispersed.

Other Food Items

The faecal data revealed the presence of soil in the diet. This may be ingested to reduce the effects of toxins and/or digestion-inhibitors from leaves. The soil found in the dung was black, presumably that of the general forest floor. We were confident that the soil was not accidentally collected whilst picking up faeces. The chimpanzees were observed to feed on the soil of termite nests and also once from a river bank. The riverbank soil in this incident had a high clay content (pers. obs.), and the presence of footprints of ungulates suggested that animals frequently returned to the same site in the river bank to feed. We continued to monitor the site occasionally but there were no further observations of chimpanzees feeding there.

Insects were not an important part of the chimpanzees' diet. There were only four records of invertebrates in the dung samples (compared to records in 30% of samples at Lopé (Tutin et al., 1991). Chimpanzees were observed to feed on caterpillars. This was a major event during the first rainy season of 1997. Perhaps due to an extremely long and harsh dry season there was an extraordinary 'rain' of caterpillars. Herbivorous damage to vegetation was apparent. During 1998 there was no such 'feast' on caterpillars. The chimpanzees were observed to feed on termites by breaking open the termite mounds of species forming colonies just below the surface of the ground. There was no evidence either from observation or feeding remains of tools being used to extract insects. In conclusion, it appears that the chimpanzees are obtaining the majority of their protein requirements from young leaves, but will sometimes exploit resources such as abundant caterpillars.

There were no records during this study period of feeding on mammalian prey. However, Budongo chimpanzees have been observed to feed on the prey of blue duiker, blue monkey, and black and white colobus (Sonso Field Station Records). Stanford (pers comm.) noted that the frequency of hunting behaviour at Gombe shows extreme variation from year to year, which may be related to the behaviour of particular chimpanzees in the community.

6.7 Conclusions

- Sonso chimpanzee behaviour, both in terms of activity budgets and diet composition, responded to variations in food availability.
- In times of food scarcity, the chimpanzees decreased the amount of time spent feeding and either fed on lower quality foods or increased the time spent moving in order to incorporate seeds and fruit in the diet.
- *Ficus mucuso* was the most highly preferred food item, in contrast to other studies where Ficus spp. are general considered as low quality and key stone food items.
- The proportion of young leaves and pith in the diet were negatively correlated with the proportion of fruit in the diet and with measures of food availability, indicating there use as keystone food items.
- Young leaves were not only keystone foods but *C. mildbraedii* young leaves were a highly preferred food item whenever available.
- Insects were not an important source of protein.
- Chimpanzees were identified as seed dispersers for 17 species of tree, and as seed predators of *Cynometra alexandrii*.

Chapter 7

Ranging Behaviour

7.1 General Introduction

The study of individual and group ranging patterns is essential for the understanding of group dispersion and ultimately group social organisation. The study of sex differences in the use and size of home ranges will aid the understanding of the potentially different foraging and association strategies of the sexes. In addition, identification of sex differences in the location of individual home ranges within a group or community home range sheds light on issues of community membership. The study of ranging behaviour can give an insight into the behavioural response of primates to changes in environmental conditions. Primates have been shown to alter their ranging patterns in response to changes in resource availability (Terborgh, 1983). In times of food scarcity primates may either extend their ranging patterns and continue to feed on high-quality food items or they may reduce the distance travelled and feed on lower-quality food items. Doran (1997) found that Tai chimpanzees reduced their day range and party size, and spent more time feeding, and on lower-quality food items. Similarly, areas of high resource abundance should result in relatively smaller community range areas and thus an increased encounter rate between community members. The documentation of the ranging patterns of different populations of the same species in different habitats will reveal the breadth of behavioural diversity within a species and also help elucidate the relationship between resource availability and distribution and a species social organisation.

The home range of an individual may be defined as the area within which an animal moves whilst performing its normal daily activities (Burt, 1943 cited in White & Garrott, 1990). The emphasis in this statement is "normal". The home range is not usually considered to be all of the area that an animal traverses in its lifetime, but the area of normal use. It is important that the time period over which the range is estimated has biological significance. It is usually impractical to collect data over the

life time of an individual, but seasonal differences etc. must be considered. The age and sex of the animal are other factors that can influence ranging patterns. It is essential that all ranging studies state all of these variables in order that comparisons may be made. Core areas are defined as areas within the home range which are used more frequently than any other area. They probably will include home sites, refuges and the most dependable food resources. Although home ranges may overlap it is possible that core areas may be areas of exclusive use. Thus these areas may be important when studying interactions between individuals and with the environment (Samuel et al., 1985).

Previous Chimpanzee Ranging Studies.

The size of chimpanzee community ranges varies between study sites (see Table7.1). These differences may be the result of differences habitat and community structure. Sex differences in chimpanzee ranging patterns were first systematically studied at Gombe (Wrangham, 1975, 1979b; Wrangham & Smuts, 1980; Goodall, 1986). Wrangham (1979b) plotted individual ranging patterns onto a 100 x 100m grid of the study area and from this calculated the annual ranges of individuals. A dichotomy between the sexes was observed: adult males 9-12km^2, adult anoestrous females 5.8-7km^2 and adult oestrous females 8.3-11km^2. When in oestrus, the ranging behaviour of a female changes dramatically. Generally, oestrous females have been observed to travel more widely within the community range and to associate in larger subgroups (Goodall, 1986). At Gombe, oestrous females have also been observed to form sexual consortships with an adult male and travel away from the main chimpanzee community and in addition, migrate to a neighbouring community (Tutin, 1979). Wrangham (1975, 1979b) found a difference in the distance travelled per day between the sexes (mean daily range length; males 4.9km; females 3km). Males tended to range more widely, visiting each of the boundary areas of the community home range once every four days or so, whereas females spent more time in their core areas. Wrangham and Smuts (1980) described the use of core areas of the community range by males and females. Estimates for core area sizes were made by analysing range use over at least eight days of observation for each focal individual.

For each day, the number of 0.5 x 0.5 km grid squares visited at least once was recorded and the number of days each such square was used was summed. The core area was taken to be the smallest number of grid squares accounting for 80% of the squares occupied across days. The data suggested that individual females spent most of their time in core areas about half the size of those occupied by males. Individual females did not have exclusive use of their core area, in fact different female core areas overlapped extensively.

Table 7.1 Range Areas From Other Study Communities.

Study Site	Range Area Km^2	Method	Community size	Independent Males
Budongo	6.78	MCP		16
	6.89	Fixed Kernel		16
	14.51	Adaptive Kernel		
	6.78	Cluster Analyses		
Gombe	13	500 x 500m grid	22	9
	10	500 x 500m grid	12	7
Kibale	14.9	MCP	>30	>13
	8.5	200 x 200m grid	>30	>13
	7.8	200 x 200m grid	>30	>13
Mahale	19.4	400 x 400m grid	34	11
Senegal	278-333	density and nests	>22	
Tai	16.5	MCP	15	3
	26.9	MCP	41	7
	19.5	MCP	46	9

community size = the number of independent individuals; MCP = minimum convex polygon.
Data Sources: Budongo, (Newton-Fisher, 1997); Gombe, (Wrangham, 1979b); Kibale, (Chapman & Wrangham, 1993); Mahale, (Hasegawa, 1990); Senegal, (Baldwin et al., 1982); Tai, (Boesch & Boesch-Achermann, 2000).

Sex differences in ranging patterns at Mahale are generally in agreement with those found at Gombe except the differences are not so pronounced (Uehara, 1981; Kawanaka, 1984; Hasegawa, 1990). It is suggested that food availability is greater at Mahale and that consequently travel costs are lower for females (Hasegawa, 1990). However, qualitative data on food abundance and distribution is not available for either site. Data from forested habitats, an assumed food richer habitat, is inconsistent. Studies at Kibale Forest have also highlighted the differences in ranging behaviour between the sexes. Males were found to have range sizes 1.5 times larger than those of females and to be seen more frequently in community boundary areas (Chapman & Wrangham, 1993). At Tai Forest however, Boesch (1991) describes

females ranging extensively throughout the community's range, in dispersed groups that include on average 72% of all community members. More studies from forested habitats are needed to assess the cause for this variation. Sex differences in the ranging patterns of *P.paniscus* have not been examined in detail, however, preliminary data suggests variation between communities. At Lomako, non-cycling females are not thought to have smaller core areas whereas at Wamba there is evidence that all females except young nulliparous ones generally use smaller areas than the males (Kitamura, 1983; White & Lanjouw, 1992).

Territorial Defence

The defence of community territories involves cooperation between community members, a strategic decision making process on when to attack and when to flee and an anticipation of future benefits after the outcome of the attack, i.e. access to fertile females. Male community members do not transfer from their natal community. This results in all male community members being kin-relations and thus reinforces the strong bonding and cooperation between males. Male members of one community will defend their territory against that of another community. The nature of the aggression shown between chimpanzees has led for some authors to compare it to that of human warfare (Wrangham & Peterson, 1996; Boesch & Boesch-Achermann, 2000; Wrangham, 1999). The strategies of attack used varies between communities (Boesch & Boesch-Achermann, 2000; Stanford, pers. comm.). At Gombe and most likely at Mahale, one community has been progressively annihilated through repetitive lethal aggressive attacks on males from a neighbouring community (Goodall et al., 1979, 1986; Nishida et al., 1985).

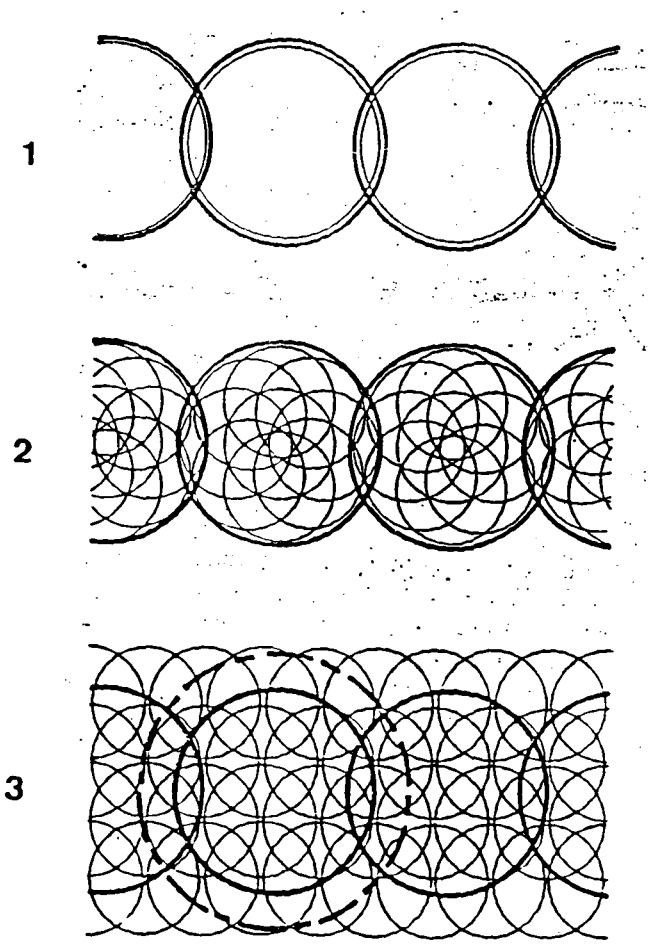
Models of Chimpanzee Dispersion

Wrangham (1979b) discusses three possible models of chimpanzee dispersion (see Fig 7.1). Models 1 and 2 propose a bisexual community, The 'classic' model proposed by Itani & Suzuki (1967) shows both males and females sharing the home range equally (model 1); model 2 shows individual female ranges to be smaller than those of males and situated within the home range of all males. On the other hand,

model 3 suggests that female ranges are smaller and that they are distributed independently of the male range. In this scenario the community concept can only be applied to males.

The data on the sex dichotomy in daily range length and core area size precludes the consideration of model 1 as an accurate description of chimpanzee social organisation. Thus, the question remains whether model 2 or model 3 is the most appropriate. Evidence exists in support of both models. Wrangham (1979b) summarised the data available at that time and concluded that the evidence suggested model 3 to be the most appropriate. Following the split of one community into two distinct male communities, females continued, at least in the beginning, to associate

Fig 7.1 The Different Models Of Chimpanzee Social Organisation (From Wrangham, 1979b). (in each diagram circles with thick lines are the male range, circles with thin lines are the female range/core areas. In (3) the dashed line shows the expansion of the male range: consequently the males associate with more females, this would not happen in (1) or (2) where females would also expand their core areas).



with both communities. Subsequent data from Mahale (Uehara, 1981; Kawanaka, 1984; Hasegawa, 1990) and also Kibale (Chapman & Wrangham, 1993) suggested that model 2 was the most appropriate. Arguments against the Wrangham-all-male community model came from other researchers at Gombe (Pusey, 1980; Goodall,

1983). They stressed that peaceful interactions between two communities were rare, that females also accompanied males on border patrols and that males have been observed to direct aggression at stranger females. However, there is still some evidence to support model 3. Recent genetic analyses of individuals of the Tai community report that 50 % of offspring are sired by individuals not known to be in the same community (Gagneux et al., 1997, 1999). Although this data is preliminary and needs to be supported by similar studies from other communities, it does raise doubts about the presumed closed mating system and corresponding ranging patterns in the Tai community. At Kibale Forest, seasonal differences in community membership have been described. During peaks of fruit production there were more sightings of familiar, but rarely seen, females and of completely unfamiliar females (Wrangham et al., 1996). Females were observed to visit fruiting groves both from distant parts of the community range and from other communities, in contrast to the consistent use by the other females. Stranger females were of great social interest to the males and there have been two recorded incidents of infanticide (Clark-Arcadi & Wrangham, 1999). Wrangham et al. (1996) suggest that Kibale may be an unusual situation because so few fruit items contribute to a large proportion of the diet, (but see Table 6.3, this thesis), and there are groves of fruiting trees which act as super-abundant food patches and may distort usual ranging patterns.

A recent study of male ranging behaviour at Budongo over one year found males to occupy core areas which represented about a third of their individual home ranges (Newton-Fisher, 1997). Such distinct core areas would not be predicted by any of the above models which all predict male chimpanzees ranging widely over the whole community range.

Pusey et al. (1997) have demonstrated with long term data from Gombe that dominance rank in female chimpanzees is important for life-time reproductive success. Higher ranking females were found to have significantly higher infant survival, faster maturing daughters, and more rapid production of young. The mechanism by which females compete is still unclear. Pusey et al. (1997) suggested that high rank probably influences reproductive success by helping females establish and maintain access to good foraging areas. This study will conduct preliminary

analyses on the relationship between ranging patterns and female dominance. There are two scenarios by which ranging patterns may show the effect of dominance. There may be a relationship between the size of a female's core area and her position in the dominance hierarchy. A dominant female may have access to the richest feeding area and therefore have a smaller range area. On the other hand a dominant female may have no restrictions of movement, and thus be able to access any food patch and therefore have a larger home range. Studies at Kibale found no relationship between a female's position and range size. However, a relationship between male dominance and size of range area was found. On the contrary, Newton-Fisher (1997) found no relationship between male dominance and size of range area for the Sonso community of chimpanzees.

Such detailed observations on the ranging behaviour of *P. paniscus* are not yet available. But Kitamura (1983) suggests a fission-fusion social organisation similar to *P.troglodytes*, but with subsets of females, rather than individual females occupying relatively small core areas compared to the males.

It is clear that there is a great deal of variability in ranging patterns between populations. It is necessary to investigate sex differences in the ranging patterns of individuals from other sites, in order to see the extent of variation and flexibility between habitats and populations of the same species. This may be particularly useful to aid comparisons of behavioural ecology between the two sister species *Pan paniscus* and *P.troglodytes*. Until the extent of variation and flexibility within one species is quantified it is impossible to make meaningful comparisons across species.

7.2 Aims

This study will investigate sex differences in the ranging patterns of the Sonso community of chimpanzees in order to address issues of both community membership and sex differences in association and foraging behaviour within the community and the importance of dominance in female chimpanzees. The following questions will be addressed:

1) Can males and females be considered as members of the same community?

2) Are there sex differences in the size and patterns of utilisation of individual home range areas?
3) Are the sizes of female home ranges related to dominance rank?
4) Is there a relationship between the location of a female's range in relation to those of males and female dominance.

7.3 Methodology

Techniques available for the estimation of home range area and utilisation may be divided into two categories non-probabilistic and probabilistic according to the methods used to obtain an estimate of range size from the location data points or 'fixes'.

(a) Non-Probabilistic Techniques

Two non-probabilistic techniques that are frequently used in chimpanzee range analyses are minimum area convex polygons (MCP) and grid cell analyses.

Minimum Convex Polygons.

The estimation of home range area using minimum convex polygons (MCP), involves joining the outermost points used by an individual or community together in such a way as to form the minimum or smallest convex polygon possible that encompasses all of the points. This is one of the oldest methods used and its advantages are that it is simple to calculate, there is no strict requirement for the fixes to be independent, and it is the only method which is strictly comparable between studies. For this reason, Harris et al. (1990) advocate its use in all studies. However, there are many disadvantages. The size of the home range area will continue to increase as more data are collected. This is because the range estimate obtained does not represent the normal area of use but the total area used. Also, as all fixes are treated as being of equal importance, the range size will be heavily influenced by peripheral fixes. This may result in large areas that an individual never visits being included in the range area. Most importantly, there is no indication of intensity of range use. Some of these disadvantages may be overcome by the use of concave polygons or by use of restricted area polygons (Harris et al., 1990).

Grid cells

This involves the overlaying of grid cells on to location fixes. This method is heavily influenced by the size of the grid cell and is not suitable for examining range areas where an outline technique would be best. It is however a useful method examining usage patterns within a home range. This technique is mentioned here as it is often used in chimpanzee studies (e.g. Hasegawa, 1990; Chapman & Wrangham, 1993). This technique was not used in this study as the interest of the study was the range outline.

(b) Probabilistic Techniques

The probabilistic methods of home range analysis attempt to assess an animal's probability of occurrence at each point in space, "the utilisation distribution". Initial procedures were complicated by the requirement of the animal's behaviour to fit a certain probability distribution e.g. bivariate (Harris et al., 1990). More recent techniques no longer require an individual's movements to comply with a particular probability distribution, thus making the analyses more sensitive to the real locational data.

Kernel Analyses

The Kernel methods (Worton 1989) are considered to be the most accurate predictors of the internal structure of an animal's home range (Seaman & Powell, 1996). Each location point is replaced with a kernel representing the amount of time spent at that data point. A grid or matrix is then superimposed over the location data, independent of the actual location data points. For each grid intersection an estimate of time spent or density at that point is obtained. These intersections are then connected by contours. As a result, shape is given to the home range which would be missing in parametric models which require the location data to correspond with a particular distribution. However, minor changes in the size of the smoothing parameter used in the analyses will have a large effect on the estimate of range size. This is highlighted as the primary drawback to this technique by Harris et al. (1990). RangesV (Kenward & Hodder, 1996) overcomes this problem by use of a technique called

least squares cross validation (Worton, 1989) to find the optimum smoothing parameter. However, the assumptions of continuous density distribution still tend to "balloon" contours into unused areas that border high use areas (Kenward & Hodder, 1996). Kernel analyses can be performed using three different methods of smoothing parameter; fixed, adaptive or cluster. Fixed Kernel analysis applies the same smoothing parameter to all areas and is regarded as providing the most accurate results (Seaman & Powell, 1996). Adaptive kernel analysis gives more weight to areas of low density of observations and Cluster Kernel analysis gives emphasis to areas of high density.

Core Area Analyses

Cluster analysis is used to identify core areas of usage within a range. It is useful as it will allow the investigation of multiple core areas. The two fixes which are closest together, and a third fix, are initially identified as the start of the cluster analyses. Subsequent fixes are then added to this initial cluster in order of nearest distance. If the distance of a subsequent fix to the initial cluster is greater than the distance to a potential new cluster, then a new cluster is formed. If two clusters have nearest neighbours at equal distances, the fix which joins is the one which minimises the distance to all fixes in the cluster. If the nearest neighbour is already assigned to another cluster, the two clusters join. When the required percentage of fixes has been assigned, convex polygons are drawn around each cluster and their areas summed (Kenward & Hodder, 1996). There are two methods of defining the distance between fixes; nearest neighbour and centroid rules. The nearest neighbour rule uses the distance of a fix from the nearest fix in the cluster. The centroid rule uses the mean distance of the fix to all other fixes in the cluster. Kenward and Hodder (1996) state that the nearest neighbour method generally produces the best results as animals tend to return to a location from which they make a foray. However, chimpanzee behaviour does not fit this model, therefore the centroid joining method was used in this study. In addition, a core area of range use may be identified as those areas within the home range where use exceeds that expected from a uniform distribution, using any method to calculate home range area (Samuel et al., 1985).

Problems of Auto-Correlation.

The reliability of the estimates of home range area and utilisation are dependent on the quality of location data. Often, the data violate many statistical assumptions and hence make the estimates worthless (Harris et al., 1990; White & Garrott, 1990). The independence of sequential data points is essential for many data analyses, as each location point contributes the same amount of information to the analyses. The closer in time that two location data points are taken the less likely the animal is to have moved to a new location and hence statistical independence is unlikely. All analysis techniques, except the estimate of home range area by MCP, require the use of statistically independent data points. A general rule of thumb to determine if two data points may be considered to be independent is to assess whether sufficient time has elapsed for the individual to move from one end of its home range to the other (White & Garrott, 1990). Newton-Fisher (1997) estimated that a male chimpanzee could move from one end of the community range to another within 4hours. The mean daily travel distance is less for female chimpanzees (Wrangham, 1975), therefore the unit of a day was used in this study.

Methodology used in this study

As stated in the General methodology, (Chapter 2), location data points or fixes, were collected during scan samples every 15min. Accuracy was assumed to be within 100m. This was because data points were recorded as the block in which an individual was found, which measured approximately 100m x 100m. The location point used in the analyses was the intersection of the grid cell. For purposes of analysis, the most frequent fix for each individual for each day was chosen in order to reduce the effects of autocorrelation. The fixes analysed here are from June 1997 - December 1998 (19 months). The time period over which the range was analysed was >12 months and thus long enough to account for seasonal differences in range use. Ranging patterns were only calculated for independent individuals. Unfortunately, due to limitations in data collection it was not possible to calculate daily travel distances or to calculate seasonal changes in range area. This is because

only a single data point was available each day and also the number of fixes required to reach an asymptote was high.

In order to calculate the combined home range sizes for all community males and all community females, the fixes from all individuals were combined. Duplicate fixes from the same day were removed in order to avoid problems of pseudoreplication. This resulted in a total of 691 fixes to determine the female range. 679 to determine the male range and 922 to determine the combined community range. The number of fixes per independent individual ranged from 19-191.

In accordance with previous studies at this site (Newton Fisher, 1997) and elsewhere (Wrangham & Smuts, 1980), areas of habitual use or 'core areas' were calculated using 80% of the observations for each individual or community range. Utilisation plots for each individual were also drawn in order to investigate the biological significance of using 80% of observations to define core areas.

In order to investigate the relationship between life history traits and ranging patterns, independent chimpanzees were separated in to 3 categories; Male; Cycling Females; Non-Cycling Females. A cycling female was defined as any female that had at least one full anogenital swelling during the course of the study. These females were MM, SR, JN, CL, MK, KY, KU. So, fixes used to measure core area for these females were not confined to periods when they were in oestrus.

7.4 Analyses.

The programme RangesV (Kenward & Hodder, 1996) was used to analyse home range size. Initially, MCP analyses were carried out which included the total number of fixes collected during 15 min scan sampling. This allowed the examination of the outer edges of the range but gives no indication of habitat utilisation. This method is not affected by problems of autocorrelation. However, in order to examine habitat utilisation and its effects on range area, it is necessary to have non- autocorrelated data. Therefore the data set was reduced to a single location fix per day in order to perform the following analyses: MCP, Fixed Kernel Analyses, Adaptive Kernel Analyses and Cluster Analyses. Analyses were also carried out to look at the percentage of overlap between individual ranges. Mann Whitney U tests were used to

compare differences between females and males and cycling females and non-cycling females.

7.5 Results

In total, 5296 scans were collected with corresponding ranging data. This data set was reduced to a single location data point or 'fix' per day per individual for a total of 289 days. The number of fixes per individual varied greatly (mean 120.34, median 129, range 19-191). There were significant differences between the median number of fixes per male compared to that per female. Mean no of fixes per female 103.67, median 113.5, range 19-175; males mean 145.43, median 129, range 95-191 (Mann Whitney U; male n=16; female n=19; z= -2.65; U= 72, $p<0.01$). This is due to problems encountered in locating some of the females.

The different analytical techniques produced different estimations of total range use and core area usage. This was expected, because range analysis techniques were chosen which emphasised different qualities of home range area and habitat utilisation. Nevertheless, all methods were significantly correlated with each other (Kendal's Coefficient of Concordance n=3, W=0.8472 chi sq 83.8698, df 33 $p<0.001$; for MCP100, KF100, KA100). It was not possible to determine which method is the most accurate reflection of 'real' ranging patterns. However the agreement between methods suggests that the differences between individuals revealed by each analysis technique are real.

Incremental plots for the estimation of home range size (based on MCP analyses) were plotted for each individual (see Appendix D.1). Figs 7.2 & 7.3 show summary data for all females and all males, the vertical bars represent individual variance. All fixes were added in the sequence in which they were collected. They show that for the majority of individuals an asymptote was reached. Nevertheless, the number of observations, (N), was significantly correlated with estimates of range size in all of the analyses of home range size (Spearman Rank $r_s = 0.72$, $P<0.001$ (MCP); $r_s = 0.76$, $p<0.001$ (MCPall); $r_s = 0.70$, $p<0.001$ (KF); $r_s = 0.57$, $p<0.001$ (KA); $r_s = 0.69$, $p<0.001$ (CA)). However, analysis of the relationship between core area size and the number of observations showed that only those using the MCP were

significantly correlated (r_s = 0.52, p=0.001). Values obtained from all other methods of analyses of core areas were not significantly correlated with the number of observations. For female ranges only, there was no significant correlation between the number of observations and the resultant range area for calculations of core areas. Calculations of male home ranges showed no significant correlation between the number of observations and either home range or core area size. This is probably a result of obtaining proportionately more location data points for male individuals. In the following analyses only the size of core areas will be used in comparisons between individuals and sexes.

Utilisation plots were examined to test the biological significance of the 80% of observations being used to represent an individuals core area, see Fig 7.3 (females), D.4 (males) and Appendix D.3 for individual female utilisation plots. Individual male utilisation plots are not shown as there was less variance between individuals. Males generally showed no obvious core area of preferred usage. Within females there was a lot of variation between individuals in the patterns of utilisation of home range area. Some females, mainly females with infants, had definite core areas of range usage which corresponded well to the estimate of 80% of observations, whereas the females later identified as peripheral, and cycling females, show less obvious patterns of core area usage. In the case of the peripheral females this is probably a result of the majority of their sightings being when they have perhaps left their core area in order to associate with other community members.

Community Range

The total range area, or 'community range', for the Sonso community of chimpanzees during this study period was estimated to be MCP 9.71km^2; KF 9.19km^2; KA 18.21km^2; CA 7.77km^2 (Table 7.2). The total range area for all females is completely overlapped by that of the males when all observation points are considered. When examining the areas of core use for all males and females, the majority of the female home range is covered by that of the males (Table 7.3). The slight discrepancies are probably due to the reduced data set, containing only the most frequent data point for each day.

Fig 7.2 Graph Of Relationship Between The Number Of Observations And Range Size For All Females, Showing Variance (y axis = the percentage of home range).

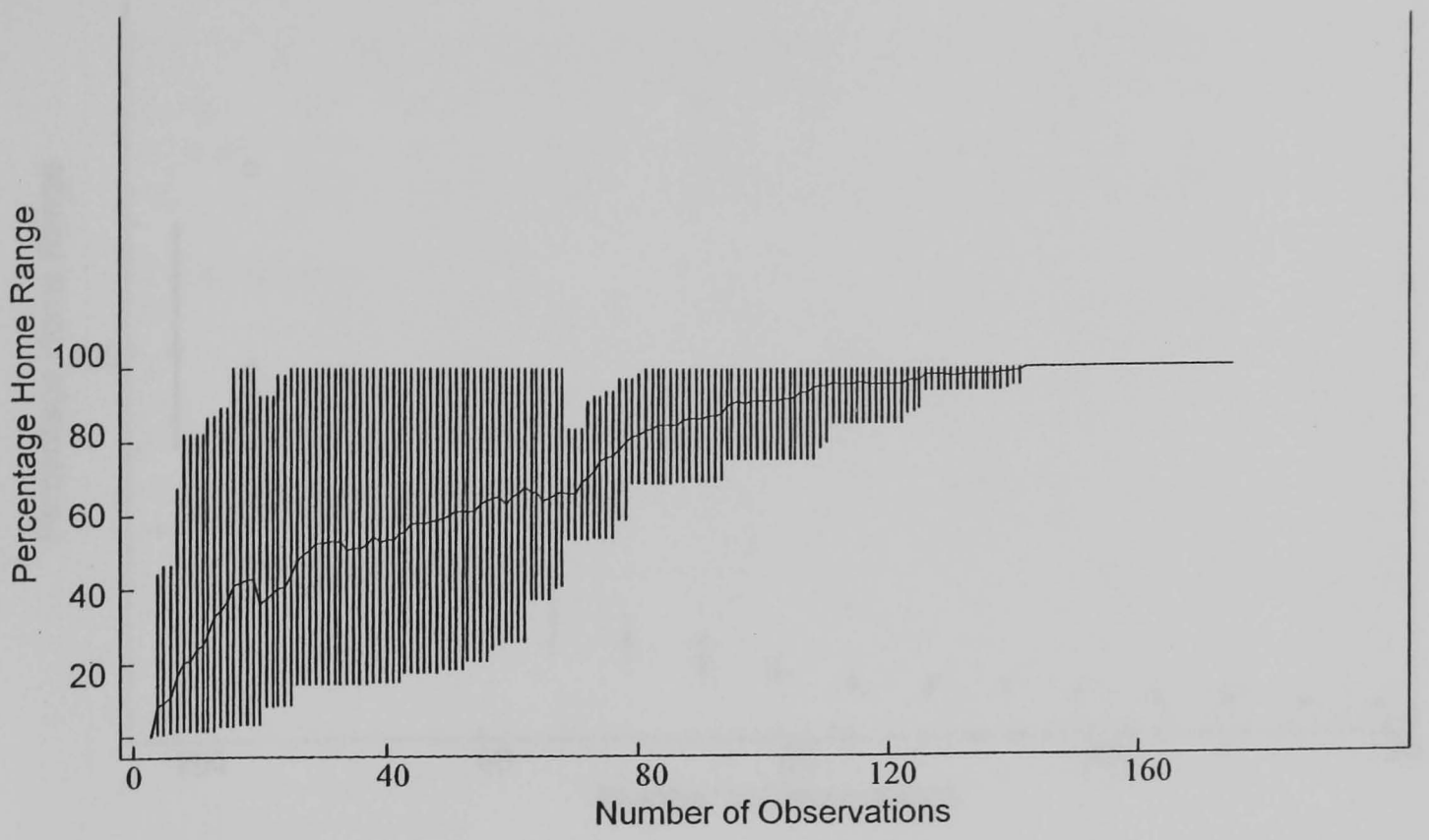


Fig 7.3 Graph Of The Relationship Between The Number Of Observations And Range Size For All Males, Showing Variance.

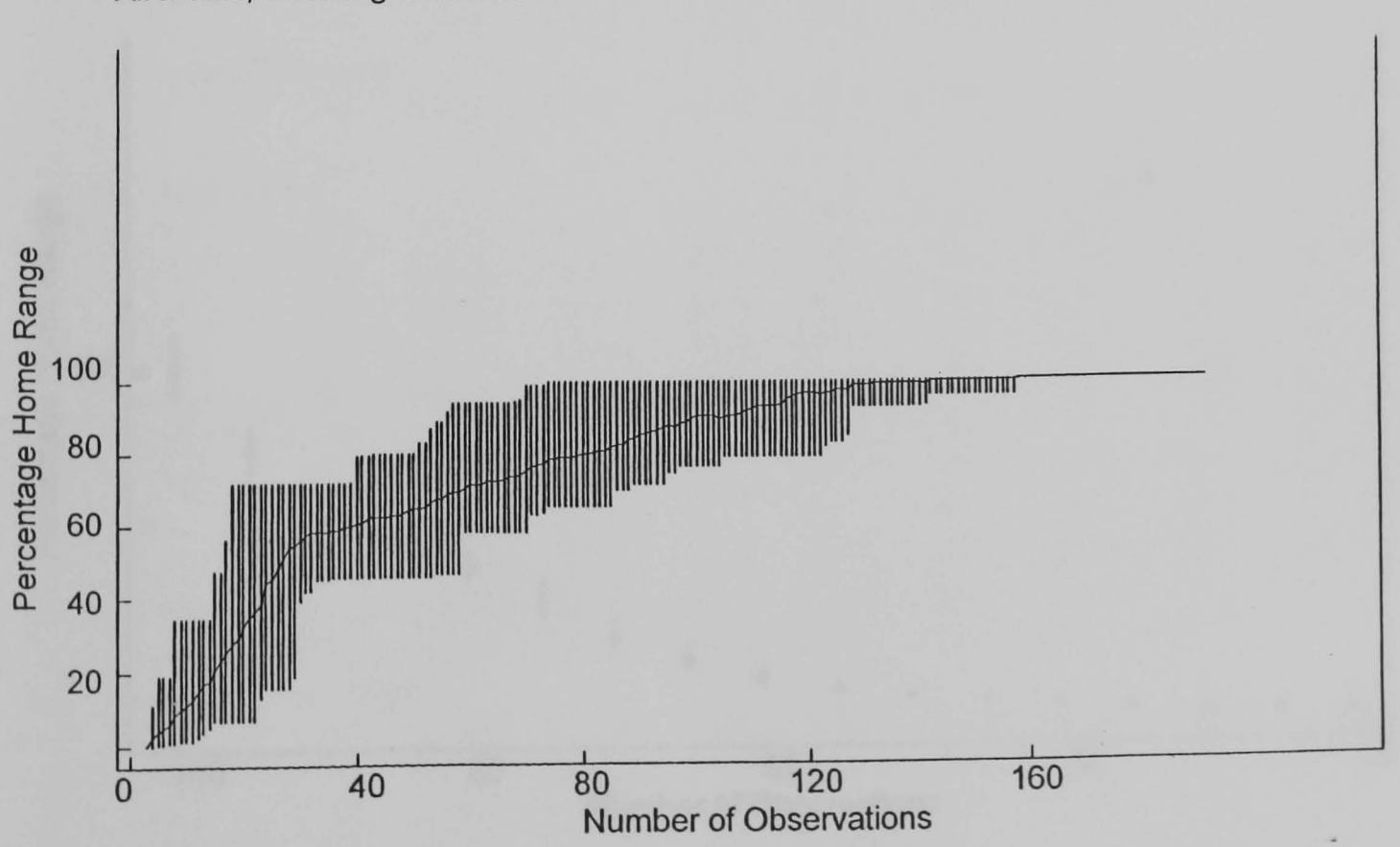


Fig 7.4 Graph Showing Patterns Of Utilisation Of Range Area For All Individual Females Combined, Showing Variance (y axis = percentage of home range).

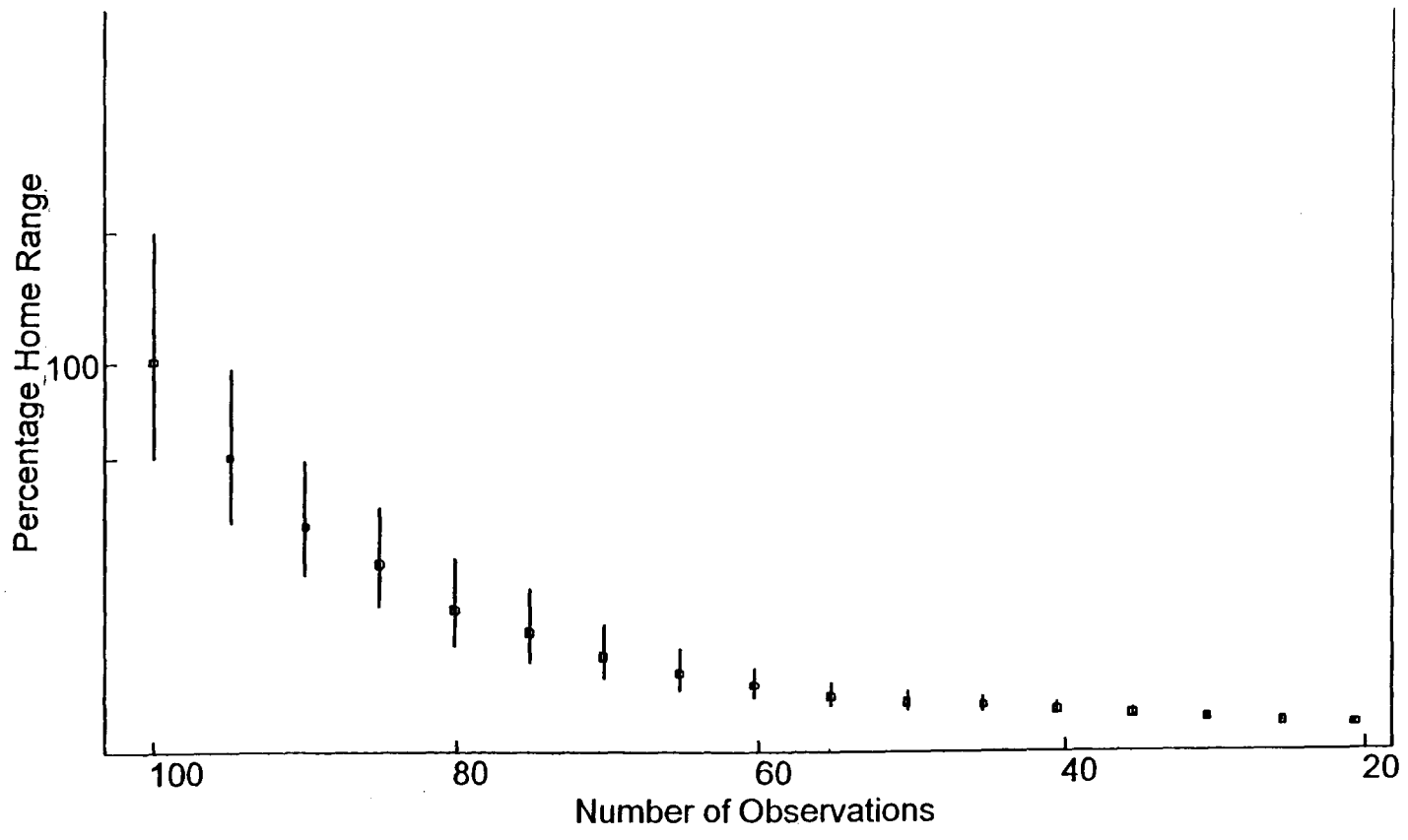


Fig 7.5 Graph Showing Patterns Of Utilisation Of Range Area For All Individual Males Combined, Showing Variance.

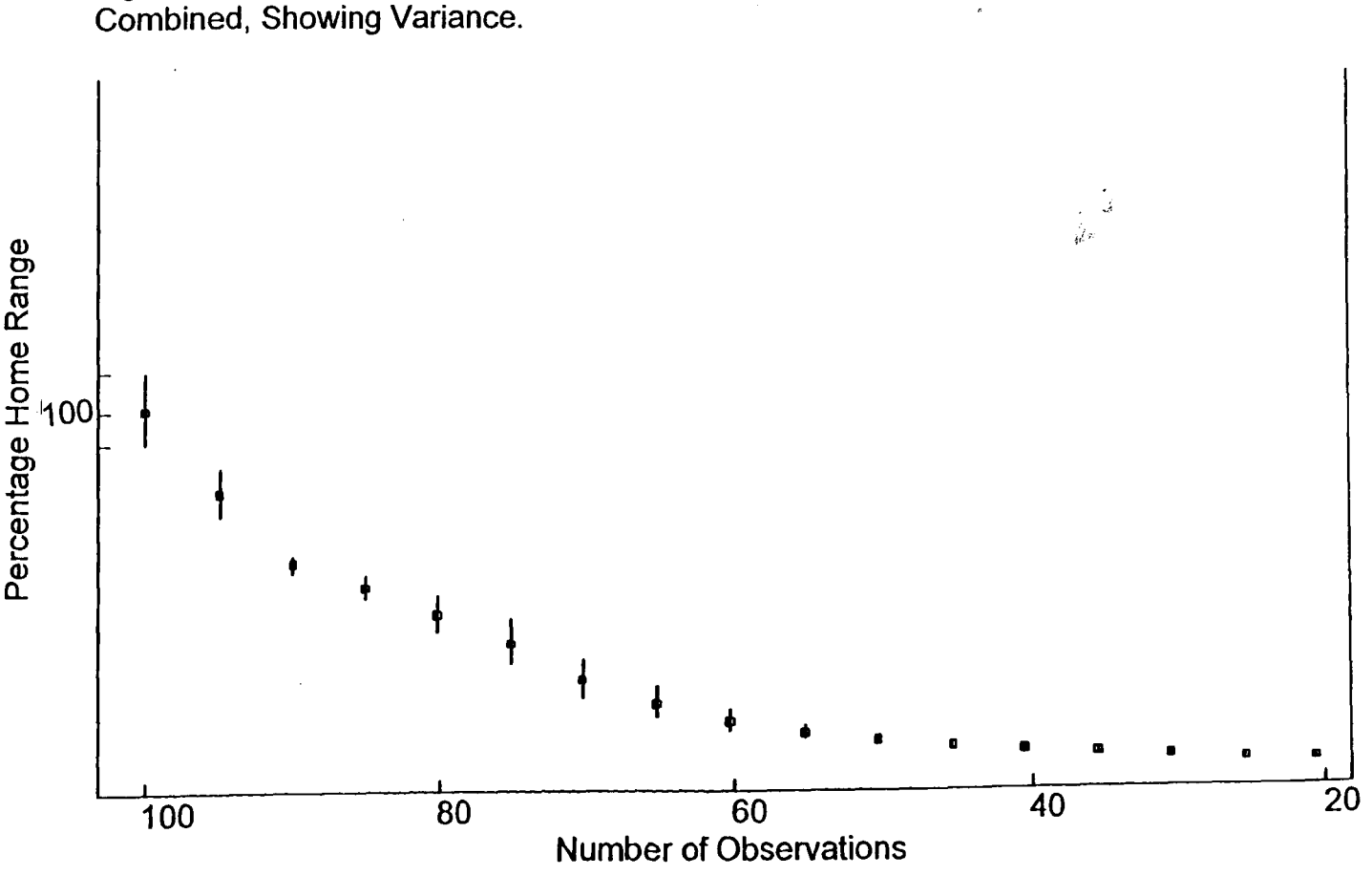


Table 7.2 Total Home Range Area(Ha) And Percentage Of Community Range For All Independent Community Members, Calculated Using Four Techniques Minimum Convex Polygon (MCP), Fixed Kernel (KF), Adaptive Kernel (KA) and Cluster Analysis (CA). (*= cycling female).

Indiv.	N	MCPall	MCP100	% com	KF100	%com	KA100	%com	CA 100	%com
All Fem.	691	883.5	859.5	88.7	928.7	101.0	1415.5	77.7	859.5	110.6
All Male.	679	971.5	966.0	99.7	951.4	103.5	1812.3	99.5	876.0	112.7
All	922	971.5	968.5	100.0	919.3	100.0	1821.8	100.0	777.0	100.0
Adult Females										
BN	38	563.0	562.0	58.0	821.8	89.4	991.3	54.4	562.0	72.3
HT	33	70.5	70.5	7.3	89.9	9.8	93.9	5.2	70.5	9.1
KL	124	444.5	441.5	45.6	396.1	43.1	1057.9	58.1	441.5	56.8
KG*	111	480.0	478.5	49.4	388.8	42.3	1018.3	55.9	478.5	61.6
KU*	116	615.0	568.5	58.7	769.8	83.7	1007.9	55.3	568.5	73.2
KW	154	556.5	512.5	52.9	507.5	55.2	920.7	50.5	512.5	66.0
MM*	19	448.0	429.0	44.3	694.2	75.5	853.8	46.9	429.0	55.2
NB	164	551.0	535.5	55.3	729.2	79.3	964.8	53.0	535.5	68.9
RD	58	149.5	149.5	15.4	145.0	15.8	266.5	14.6	149.5	19.2
RH	62	464.0	457.5	47.2	706.4	76.8	1064.0	58.4	457.5	58.9
ZA	68	348.5	348.5	36.0	462.1	50.3	933.4	51.2	348.5	44.9
ZM	139	410.5	410.0	42.3	475.9	51.8	1042.0	57.2	410.0	52.8
Adolescent Females										
CL*	158	813.5	742.5	76.7	1050.3	114.3	1421.7	78.0	742.5	95.6
JN*	175	798.5	729.5	75.3	896.7	97.5	1025.7	56.3	729.5	93.9
KY*	158	513.0	441.5	45.6	556.1	60.5	729.0	40.0	441.5	56.8
MK*	129	631.0	591.5	61.1	613.7	66.8	965.0	53.0	591.5	76.1
SR8	96	496.5	479.0	49.5	427.1	46.5	923.4	50.7	479.0	61.6
VT	19	114.5	114.5	11.8	230.0	25.0	267.4	14.7	114.5	14.7
Juvenile Female										
JF	64	504.5	501.5	51.8	171.9	18.7	1270.0	69.7	501.5	64.5
Adult Males										
BK	160	739.5	604.5	62.4	791.5	86.1	948.6	52.1	604.5	77.8
BY	119	846.5	809.0	83.5	672.0	73.1	1149.9	63.1	809.0	104.1
DN	167	929.0	842.0	86.9	961.7	104.6	1685.7	92.5	842.0	108.4
JM	95	567.0	465.0	48.0	516.3	56.2	688.3	37.8	465.0	59.8
MA	167	938.0	864.0	89.2	964.1	104.9	1733.9	95.2	864.0	111.2
MG	170	880.0	871.5	90.0	1088.7	118.4	2134.7	117.2	871.5	112.2
MU	142	694.0	665.0	68.7	826.2	89.9	1008.6	55.4	665.0	85.6
NJ	167	894.0	788.5	81.4	976.3	106.2	1623.6	89.1	788.5	101.5
TK	103	680.0	646.5	66.8	822.5	89.5	868.0	47.6	646.5	83.2
VN	140	945.0	911.0	94.1	795.9	86.6	1409.9	77.4	911.0	117.2
ZT	165	874.5	825.5	85.2	1033.0	112.4	2094.2	114.9	825.5	106.2
Adolescent Males										
AY	191	772.5	618.0	63.8	839.3	91.3	853.7	46.9	618.0	79.5
NK	121	857.0	831.5	85.9	912.8	99.3	1914.1	105.1	831.5	107.0
BB	149	592.0	556.5	57.5	684.8	74.5	1273.0	69.9	556.5	71.6
ZF	121	773.5	761.0	78.6	935.1	101.7	1220.1	67.0	761.0	97.9
Juvenile Males										
GS	150	749.5	723.5	74.7	907.1	98.7	1337.9	73.4	723.5	93.1

Table 7.3 Range Overlap Between The Total Female Range And The Total Male Range.

Percentage Overlap	MCP (all scans)	MCP80	KF80	KA80	CA80
male range overlap female range	100	99.5	97.9	95.8	99.7
female range overlap male range	90.8	76	82.9	86.1	88.6

The relative community range area for different communities inhabiting different habitats was investigated. Only results from studies having habituated communities are used. Both the number of independent community members and the number of independent males in a community were used to index the community range size, resulting in the measurements of relative community range area (Fig 7.7). There is a negative relationship between both the number of independent community members

Fig 7.6 Graph Showing The Relationship Between Number Of Observations And Community Range Size (y axis = percentage of home range area).

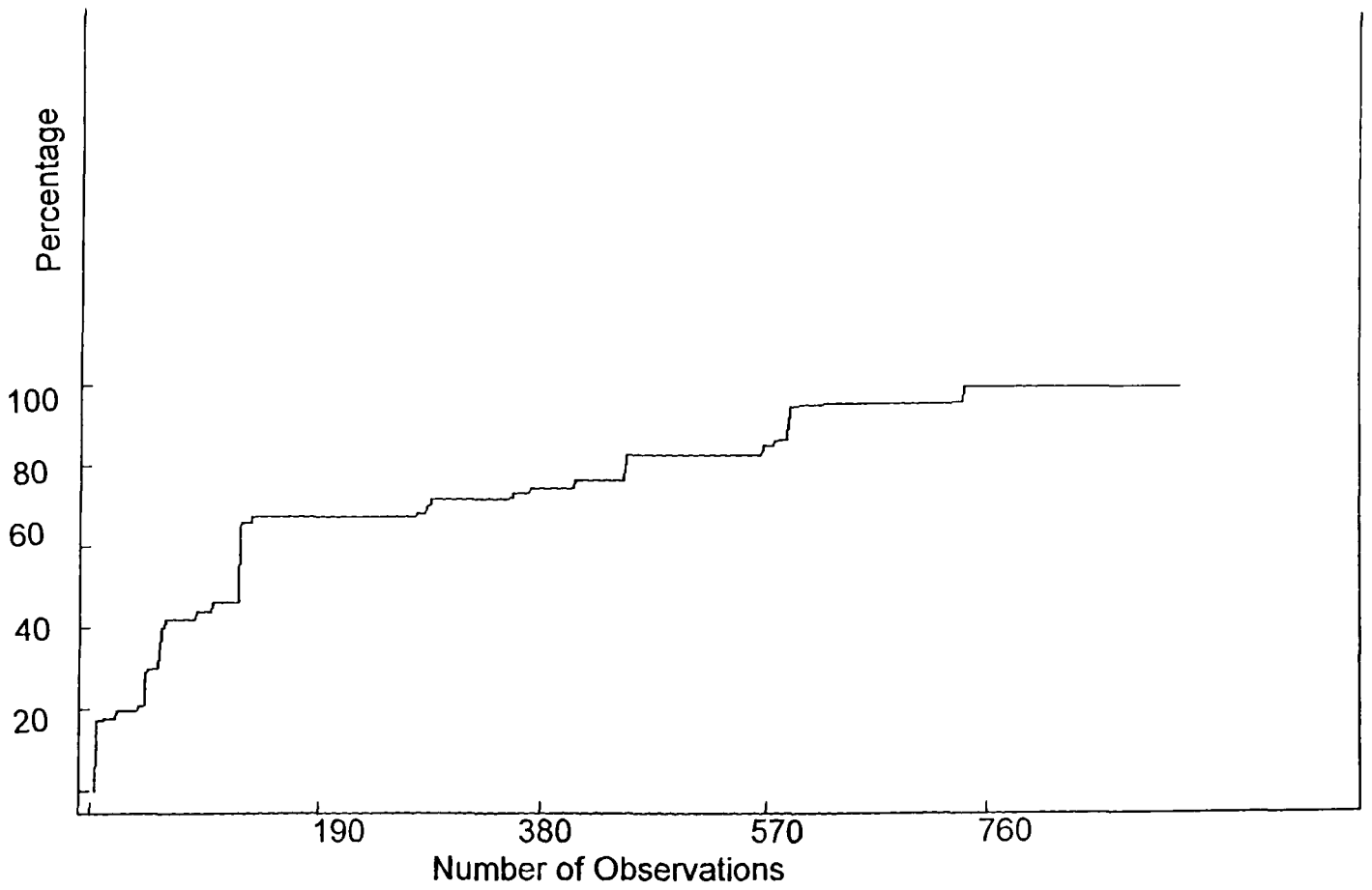
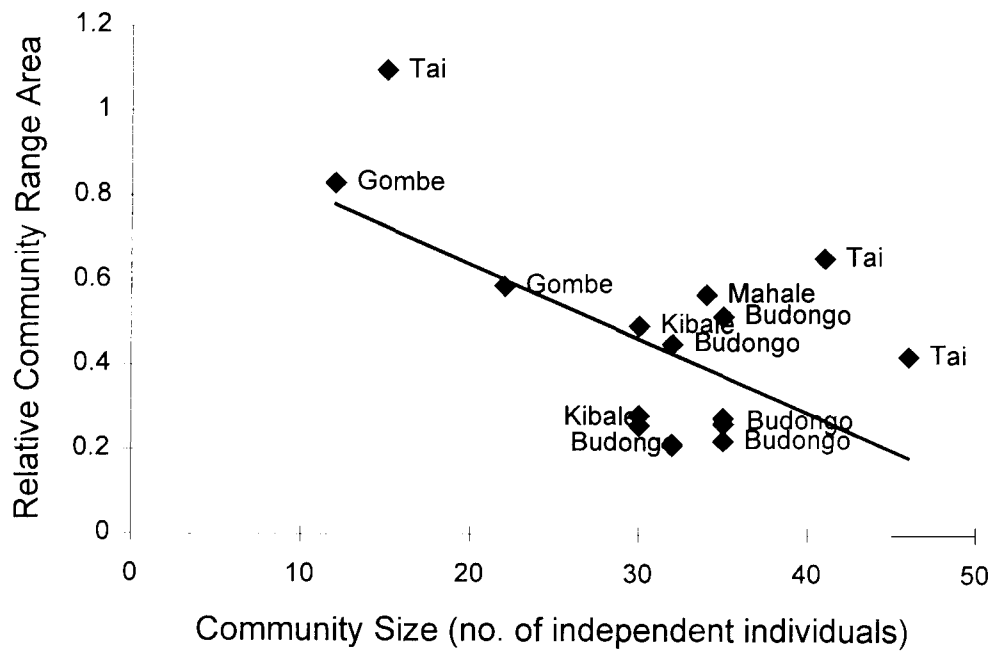
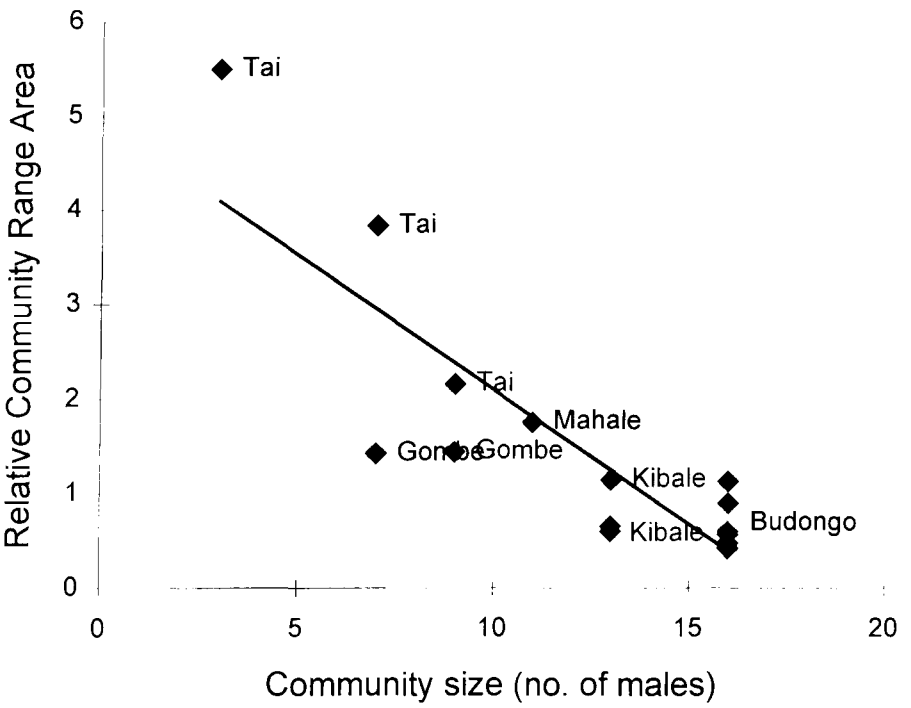


Fig 7.7 Comparison Of Relative Community Range Area Between Study Communities In Different Habitats. A) Number Of Independent Community Members B) Number Of Independent Males. (see Table 7.1 for references to source data).

a)



b)



and the number of males only and the relative community range size. From both models there appears to be a trend for the communities in forested habitats to have relatively smaller community range areas. However, the data from Tai Forest do not follow this trend.

Individual Ranges.

The range areas of individual males and females varied greatly in size (Table 7.2 & 7.4). Comparisons were made between the median sizes of the core areas and different categories of individual, see table 7.5 for summary. There are significant differences between the median size of female vs. the median size of male range for all analyses except Cluster Analyses. (Mann Whitney U test males n=16, females n=19; MCP80 U=29, z= -4.07, $p<0.001$; KF80 U=70, z= -2.72, $p<0.01$; KA80 U=86, z= -2.19, $p<0.05$). Within the female ranges there are no significant differences between the age of the female and home range size (Mann Whitney U test adult females n= 12, adolescent females n=6; MCP80 U=29, z= -0.66, ns; KF80 U=24, z= -1.12, ns; KA80 U=27, z= -0.84, ns; CA80 U= 26, z= -0.94, ns). However, there are significant differences between females of different reproductive states and home range size (Mann Whitney U test cycling females n=7, non-cycling females n= 11; MCP80 U= 14, z= -2.22, $p<0.05$; KF80 U=11, z= -2.49, $p<0.05$; KA80 U=16, z= -2.04, $p<0.05$; CA80 U=9, z= -2.67, $p<0.01$). There are no significant differences between the median home range size of adult vs. adolescent males (Mann Whitney U test adult males n=11; adolescent males n=4; MCP80 U=17, z= -0.65, ns; KF80 U=15, z= -0.91, ns; KA80 U=8, z= -1.83, ns; CA80 U=21, z= -0.13, ns). There are no significant differences between the size of male core areas and cycling female core areas except using MCP analyses (Mann Whitney U test males n= 15, cycling females n=7, MCP80 U=20, z= -2.29, $p<0.05$; KF80 U=46, z= -0.046, ns. KA80 U=43, z= -0.67, ns; CA80 U=30, z= -1.5860, ns).

Table 7.4 Core Areas(Ha) And % Of Individual And Community Home Range For All Independent Community Members, Calculated Using Four Techniques Minimum Convex Polygon (MCP), Fixed Kernel (KF), Adaptive Kernel (KA) and Cluster Analysis (CA). (*=cycling female)

Indiv.	N	MCP80	ind%	cr%	KF80	ind%	cr%	KA80	ind%	cr%	CA80	ind%	cr%
All Fem	691	259.5	30.2	26.8	186.9	20.1	20.3	198.4	14.0	10.9	77.0	9.0	9.9
All Mal.	679	341.5	35.4	35.3	221.7	23.3	24.1	220.8	12.2	12.1	186.0	21.2	23.9
ALL	922	300.5	31.0	31.0	198.5	21.6	21.6	197.0	10.8	10.8	97.0	12.5	12.5
Adult Females													
BN	38	269.0	47.9	27.8	280.4	34.1	30.5	295.8	29.8	16.2	66.5	11.8	8.6
HT	33	33.0	46.8	3.4	39.7	44.2	4.3	51.4	54.7	2.8	10.5	14.9	1.4
KL	124	79.5	18.0	8.2	89.0	22.5	9.7	92.7	8.8	5.1	49.0	11.1	6.3
KG*	111	66.0	13.8	6.8	80.8	20.8	8.8	87.9	8.6	4.8	50.0	10.4	6.4
KU*	116	281.0	49.4	29.0	276.5	35.9	30.1	288.3	28.6	15.8	113.5	20.0	14.6
KW	154	68.0	13.3	7.0	105.3	20.7	11.5	104.2	11.3	5.7	61.5	12.0	7.9
MM*	19	215.5	50.2	22.3	343.7	49.5	37.4	329.8	38.6	18.1	215.5	50.2	27.7
NB	164	267.0	49.9	27.6	249.8	34.3	27.2	313.2	32.5	17.2	116.5	21.8	15.0
RD	58	50.5	33.8	5.2	51.3	35.4	5.6	59.8	22.4	3.3	19.0	12.7	2.4
RH	62	231.5	50.6	23.9	257.8	36.5	28.0	289.1	27.2	15.9	108.5	23.7	14.0
ZA	68	88.0	25.3	9.1	92.3	20.0	10.0	118.4	12.7	6.5	38.0	10.9	4.9
ZM	139	74.5	18.2	7.7	95.1	20.0	10.3	92.3	8.9	5.1	47.5	11.6	6.1
Adolescent Females													
CL*	158	258.0	34.7	26.6	265.2	25.3	28.9	266.6	18.8	14.6	176.5	23.8	22.7
JN*	175	365.0	50.0	37.7	323.8	36.1	35.2	306.4	29.9	16.8	161.0	22.1	20.7
KY*	158	160.0	36.2	16.5	144.9	26.1	15.8	156.2	21.4	8.6	61.0	13.8	7.9
MK*	129	173.0	29.2	17.9	174.1	28.4	18.9	196.3	20.3	10.8	101.0	17.1	13.0
SR*	96	117.5	24.5	12.1	129.6	30.4	14.1	207.9	22.5	11.4	86.5	18.1	11.1
VT	19	46.5	40.6	4.8	107.1	46.5	11.6	123.0	46.0	6.8	28.0	24.5	3.6
Juvenile Females													
JF	64	198.0	39.5	20.4	97.1	56.5	10.6	258.1	20.3	14.2	120.0	23.9	15.4
Adult Males													
BK	160	340.0	56.2	35.1	260.0	32.9	28.3	259.7	27.4	14.3	68.0	11.2	8.8
BY	119	389.0	48.1	40.2	253.2	37.7	27.5	298.6	26.0	16.4	68.5	8.5	8.8
DN	167	361.0	42.9	37.3	280.3	29.1	30.5	305.0	18.1	16.7	115.5	13.7	14.9
JM	95	276.5	59.5	28.5	175.0	33.9	19.0	274.8	39.9	15.1	147.5	31.7	19.0
MA	167	341.0	39.5	35.2	297.0	30.8	32.3	296.4	17.1	16.3	84.0	9.7	10.8
MG	170	338.5	38.8	35.0	257.4	23.6	28.0	250.8	11.8	13.8	78.0	9.0	10.0
MU	142	329.5	49.5	34.0	318.6	38.6	34.7	299.9	29.7	16.5	81.5	12.3	10.5
NJ	167	366.0	46.4	37.8	305.4	31.3	33.2	312.2	19.2	17.1	57.0	7.2	7.3
TK	103	178.5	27.6	18.4	238.8	29.0	26.0	265.4	30.6	14.6	134.5	20.8	17.3
VN	140	385.5	42.3	39.8	314.0	39.4	34.2	290.1	20.6	15.9	85.0	9.3	10.9
ZT	165	299.5	36.3	30.9	291.2	28.2	31.7	285.1	13.6	15.6	141.5	17.1	18.2
Adolescent Males													
AY	191	280.5	45.4	29.0	229.1	27.3	24.9	225.1	26.4	12.4	107.5	17.4	13.8
NK	121	348.5	41.9	36.0	258.9	28.4	28.2	262.1	13.7	14.4	84.5	10.2	10.9
BB	149	187.0	33.6	19.3	193.6	28.3	21.1	210.1	16.5	11.5	65.5	11.8	8.4
ZF	121	346.5	45.5	35.8	310.0	33.2	33.7	291.7	23.9	16.0	103.5	13.6	13.3
Juvenile Males													
GS	150	316.5	43.7	32.7	262.0	28.9	28.5	259.6	19.4	14.3	72.0	10.0	9.3

Table 7.5 Average Core Area Size (Ha) For Non-Cycling And Cycling Females And Males.

	Non-Cycling Females				Cycling Females				Males			
	MCP	KF	KA	CA	MCP	KF	KA	CA	MCP	KF	KA	CA
Mean	127.7	133.1	264.1	57.4	204.5	204.5	229.9	120.6	317.8	317.8	274.2	93.4
Median	79.5	97.1	118.7	49	194.3	219.6	237.3	107.3	339.3	261	280.	84.3
St.Dev	93.2	86.1	336.1	34.8	95.9	95.9	82.6	58.4	61.7	61.7	28.9	28.5
Min	33	39.7	51.4	10.5	66	66	87.9	50	178.5	178.5	210.1	57
Max	269	80.4	1230	116.5	365	365	39.8	215.5	389	389	312.3	147.5
N	11	11	11	11	8	8	8	8	16	16	16	16

The mean percentage of an individual home range which was classified as a core area was 16.22 - 39.12% depending on the analysis used (Table 7.6). There were no significant differences in the percentage of total individual home range area used as a core area between the different categories of individuals namely, non-cycling females, cycling females and males, except when using Cluster Analyses to compare non-cycling females and males (Mann Whitney $U=16$, $z= -2.03$, $p<0.05$). This probably highlights the difference between mono-core and multi-core analysis techniques. The mean percentage of the community home range which was used as a core area was between 11.48 - 32.97% (see Table 7.7).

Table 7.6 Mean Percentage Of Individual Home Range Area Which Is Individual's Core Area.

	Non-Cycling Females				Cycling Females				Males			
Method	MCP	KF	KA	CA	MCP	KF	KA	CA	MCP	KF	KA	CA
mean	34.88	33.70	24.96	16.26	36.03	31.54	23.60	21.92	43.58	31.28	22.11	13.34
median	39.48	34.25	22.44	12.70	35.49	29.36	21.97	19.01	43.31	29.97	19.99	11.50
st. dev.	14.0	12.15	15.16	5.84	13.37	8.94	8.90	12.22	7.90	4.40	7.54	6.13
min.	13.7	19.98	8.76	10.90	13.80	20.78	8.63	10.45	27.61	23.64	11.75	7.23
max.	50.6	56.49	54.67	24.45	50.23	49.51	38.63	50.23	59.46	39.45	39.92	31.72

Table 7.7 Mean Percentage Of Total Community Range Area Which Is An Individual's Core Area.

	Non-cycling Females				Cycling Females				Males			
Method	MCP	KF	KA	CA	MCP	KF	KA	CA	MCP	KF	KA	CA
mean	11.85	14.32	8.12	6.96	23.16	25.76	13.73	16.82	32.82	28.88	15.1	12.2
median	7.69	10.34	5.72	6.31	22.25	28.85	14.64	14.61	35.11	4.71	15.65	10.88
st. dev.	9.47	9.45	5.47	4.31	8.68	9.45	3.53	7.09	6.6	28.28	1.63	3.72
min.	3.41	4.32	2.82	1.35	12.13	14.1	2.82	7.85	18.43	19.04	11.53	7.34
max.	27.77	30.5	17.19	14.99	37.69	37.39	17.19	27.73	40.17	34.65	17.14	18.98

The Relationship Between Dominance And Core Area Size

It was not possible to determine a precise dominance hierarchy for the Sonso community of chimpanzees (see Chapter 8). However, the relative dominance relationship between several individuals could be decided based on the outcome of pant-grunt and agonistic interactions. Table 7.8 shows groups of females whose relative dominance positions were determined, their rank position (1 = high). their core area size as determined by the four analysis techniques and the value of a Spearman rank correlation between core area size and hierarchy.

Table 7.8 Relationship Between Female Dominance And Core Area Size.

	Rank	MCP	KF	KA	CA
NB	1	267	249.8	313.2	116.5
KG	2	66	80.8	87.9	50
KU	3	281	276.5	288.3	113.5
KL	4	79.5	89	92.7	49
ZA	5	88	92.3	118.4	38
r_s		-0.1; n.s.	-0.1; n.s.	-0.3; n.s.	-0.9; $p<0.05$
NB	1	267	249.8	313.2	116.5
BN	2	269	280.4	295.8	66.5
MM	3	215.5	343.7	329.8	215.5
ZA	4	88	92.3	118.4	38
r_s		-0.8; n.s.	-0.2;n.s.	-0.4; n.s.	-0.4; n.s.
ZM	1	74.5	95.1	92.3	47.5
KL	2	79.5	89	92.7	49
RH	1	231.5	257.8	289.1	108.5
KL	2	79.5	89	92.7	49
KY	1	160	144.9	156.2	61
JN	3	365	323.8	306.4	161
SR	2	117.5	129.6	207.9	86.5
CL	4	258	265.2	266.6	176.5
r_s		1.00, n.s.	1.00, n.s.	0.60, n.s.	0.20, n.s.
KY	1	160	144.9	156.2	61
EM	2	198	97.1	258.1	120
MK	1	173	174.1	196.3	101
CL	2	258	265.2	266.6	176.5

Table 7.9 Percentage Overlap between Individual Female Core areas and the core area of the all-males range. (Individuals in columns ranges overlap individuals in rows) using Fixed Kernel analysis

	All-Male	BN	HT	KL	KG	KU	KW	MM	NB	RD	RH	ZA	ZM	CL	JN	KY	MK	SR	VT	EM
All-Male		81.3	18.5	40.3	36.7	97.7	47.6	82.6	95.8	23.5	95.8	41.9	43.0	94.4	100.0	64.8	73.4	58.9	47.6	40.0
BN	64.3		14.6	31.9	29.1	71.6	35.9	90.4	70.6	18.6	72.8	31.2	32.5	73.0	75.0	47.2	57.6	42.1	36.3	29.5
HT	100.0	100.0		97.8	70.7	100.0	73.6	97.8	100.0	33.1	100.0	55.3	70.7	100.0	100.0	90.3	99.8	99.5	74.3	72.3
KL	100.0	100.0	44.2		75.7	100.0	80.4	100.0	100.0	50.7	100.0	69.5	77.7	100.0	100.0	93.1	98.9	99.8	80.1	73.2
KG	100.0	100.0	35.2	83.3		100.0	99.1	100.0	100.0	63.7	100.0	91.9	99.0	100.0	100.0	100.0	100.0	98.7	99.6	80.1
KU	78.5	72.4	14.8	32.4	29.3		38.1	74.8	89.9	18.8	82.0	33.6	34.6	89.5	98.2	52.7	61.9	47.4	38.9	31.2
KW	100.0	95.3	28.1	68.1	76.2	100.0		99.9	100.0	48.9	96.8	87.3	90.4	100.0	100.0	99.9	100.0	88.1	96.6	64.2
MM	53.4	73.8	11.7	26.0	23.7	60.3	30.9		58.2	15.1	63.0	27.1	27.8	60.2	65.4	37.7	45.3	35.7	31.4	22.1
NB	85.1	79.2	16.3	35.8	32.5	99.3	42.2	80.0		20.9	87.5	37.2	38.2	95.4	98.2	58.2	68.0	52.5	43.0	33.8
RD	100.0	100.0	25.7	87.6	100.0	100.0	100.0	100.0	100.0		100.0	100.0	100.0	100.0	100.0	100.0	100.0	99.1	100.0	87.8
RH	82.2	79.0	16.0	34.6	31.5	87.8	39.6	83.7	84.7	20.2		34.4	35.9	84.7	91.1	52.7	64.5	50.5	39.2	34.0
ZA	100.0	94.1	24.2	66.8	80.5	100.0	99.3	99.8	100.0	55.8	96.0		93.6	100.0	100.0	100.0	100.0	87.9	97.7	68.9
ZM	100.0	95.3	30.0	72.6	84.1	100.0	99.8	99.9	100.0	54.2	97.3	90.9		100.0	100.0	100.0	100.0	91.9	98.6	70.7
CL	79.0	77.1	15.5	33.8	30.6	93.5	39.9	77.9	89.8	19.7	82.4	35.1	36.1		99.4	55.0	65.9	48.4	40.7	32.5
JN	68.6	65.0	12.7	27.6	25.0	84.0	32.6	69.5	75.8	16.1	72.8	28.8	29.4	81.6		44.8	53.8	40.6	33.4	27.9
KY	98.9	91.0	25.4	57.2	56.1	100.0	72.5	88.8	100.0	35.8	93.5	63.8	65.5	100.0	100.0		95.4	77.3	71.8	55.0
MK	93.2	92.7	23.3	50.7	46.5	98.2	60.6	89.0	97.3	29.7	95.4	53.1	54.7	100.0	100.0	79.5		67.3	61.3	46.2
SR	99.7	90.1	31.0	68.3	61.4	100.0	70.9	93.7	99.9	39.4	99.4	62.3	67.0	98.1	100.0	85.4	89.8		69.4	60.8
VT	98.0	94.4	28.0	66.6	75.4	100.0	94.9	100.0	100.0	47.9	94.1	84.3	87.5	100.0	100.0	97.2	99.5	84.5		62.7
EM	89.3	83.5	30.1	66.0	65.5	87.3	68.3	76.7	85.4	46.0	88.5	64.4	67.9	86.8	90.9	80.5	81.2	80.7	68.1	

Table 7.10 Percentage Overlap between Individual Female Core areas and the core area of the all-males range. (Individuals in columns ranges overlap individuals in rows) using Cluster Analysis.

	All-Male	BN	HT	KL	KG	KU	KW	MM	NB	RD	RH	ZA	ZM	CL	JN	KY	MK	SR	VT	EM
All-Male		25.9	6.1	26.9	27.0	52.1	32.5	46.5	57.9	10.9	39.6	21.0	25.7	72.1	69.3	32.3	48.6	46.5	14.7	48.0
BN	71.8		9.0	40.4	44.3	57.1	53.1	71.8	61.8	22.5	72.1	39.1	43.5	71.8	74.9	46.4	68.8	60.9	38.6	57.0
HT	100.0	52.4		81.1	55.1	82.8	54.8	71.6	100.0	10.5	57.2	12.9	55.1	100.0	100.0	57.7	81.7	98.8	10.0	74.2
KL	100.0	54.8	17.8		90.1	95.2	79.9	80.2	93.1	36.2	77.2	58.3	78.1	92.6	99.5	74.1	97.8	98.4	46.8	90.4
KG	100.0	58.9	12.4	88.5		99.3	85.7	84.6	94.3	39.0	83.8	64.5	84.7	94.6	99.6	76.6	99.0	97.5	53.9	91.0
KU	85.4	34.1	8.1	41.1	44.0		51.4	56.8	76.5	17.4	64.1	32.7	38.4	82.8	80.2	45.9	68.3	68.8	24.9	75.1
KW	100.0	58.9	10.6	64.6	70.9	95.0		75.0	94.7	32.7	70.2	54.9	62.5	96.5	98.6	66.3	86.8	94.8	44.6	89.5
MM	40.7	22.9	4.0	18.5	20.1	30.2	21.4		30.3	8.8	34.9	11.9	18.0	43.0	35.9	17.7	33.2	26.9	12.9	27.3
NB	92.6	36.0	9.5	39.9	41.4	75.8	50.4	55.8		17.6	50.9	31.4	38.8	83.7	83.8	47.0	67.7	67.8	24.0	68.3
RD	100.0	78.4	6.0	91.0	100.0	100.0	100.0	93.8	100.0		93.6	84.2	97.7	100.0	100.0	84.2	100.0	100.0	80.0	96.8
RH	67.3	45.4	6.0	34.6	39.0	67.1	39.4	68.3	54.2	17.4		28.5	34.6	76.1	66.7	39.4	56.2	55.1	23.8	52.1
ZA	100.0	67.7	4.1	75.7	84.4	97.2	87.7	65.8	93.5	42.5	80.2		80.4	100.0	100.0	97.6	88.9	94.9	62.7	93.9
ZM	100.0	61.6	13.4	81.5	89.8	91.5	79.6	78.9	93.0	41.0	77.6	65.1		96.0	99.5	79.5	91.0	90.9	52.4	87.8
CL	77.1	27.8	6.9	26.7	27.5	53.6	33.6	51.9	55.5	11.8	47.3	22.0	26.7		66.4	34.5	45.3	47.8	15.7	42.6
JN	80.7	31.7	7.6	31.1	31.6	56.9	37.5	47.6	60.6	13.0	45.8	24.2	30.3	72.8		36.6	54.1	51.8	18.1	48.4
KY	98.5	51.0	11.0	59.2	62.5	84.1	65.3	60.2	86.7	27.4	69.3	61.1	62.3	96.5	93.2		76.7	79.9	43.3	78.2
MK	89.4	45.9	9.4	48.2	50.0	78.0	53.0	69.9	78.2	19.9	60.9	34.7	43.7	79.0	86.3	47.4		66.2	28.7	81.7
SR	99.5	47.8	12.9	56.0	56.5	90.3	66.6	66.0	89.5	23.2	69.6	41.9	50.1	95.6	95.1	56.9	76.8		30.1	76.7
VT	96.2	90.7	4.2	81.8	96.2	100.0	96.1	96.9	96.2	55.9	90.2	85.4	87.9	95.9	100.0	94.0	100.0	92.3		84.4
EM	75.7	32.2	7.2	37.7	38.1	71.2	45.8	49.1	66.8	16.6	47.4	30.1	35.2	62.9	65.7	41.0	69.7	55.4	20.1	

There is no obvious relationship between core area size and a female's position in the dominance hierarchy. None of the mono-core analyses of range area produced any significant correlations; however, cluster analysis produced significant correlations for adult females. The results using the mono-core analyses although not significant, support the general trend obtained using cluster analyses. The correlations for adult and adolescent females are in opposite directions. For adult females it appears that the higher ranking females had larger core areas. Opposing this trend, the data suggest that for adolescent females higher rank is associated with smaller range size.

Overlap Analyses.

In order to examine the percentage of range overlap between individual core areas, the range outlines produced by Fixed Kernel and Cluster Analysis were used. These two methods of calculating range outlines were judged to give the most accurate estimation of range size using a mono-core and multi-core techniques. The percentage overlap between female and male ranges within sex categories and the percentage overlap between individual female ranges and the total core area of all male ranges were calculated, see Tables 7.9 & 7.10.

Table 7.11 Mean Values Of Overlap Between Individual Male And Female Ranges.

	Method	Mean	Median	N	Minimum	Maximum	St. Dev.
Females	KF	70.84	76.90	342	11.68	100	27.46
	CA	59.87	6.00	342	3.96	100	27.69
Males	KF	86.00	89.28	240	51.25	100	12.03
	CA	74.60	75.1	240	46.1	98.88	11.00

The mean percentage overlap between female core areas was significantly less than that between males, see Table 7.11, (KF80 Mann Whitney U= 3224, z= -4.2960, $p<0.0001$; CA80 Mann Whitney U= 9247, z= -5.9056, $p< 0.0001$). There is more variance in the degree of overlap between female core areas compared to those of males. There were also wide variations in the degree of overlap between individual female core areas and the total core area of all male ranges (KF80 mean 88.95, median 97.95, minimum 53.39, maximum 100, st dev. 14.38; CA80 mean 88.16,

median 96.15, minimum 40.72, maximum 100, st dev. 15.98). The ranges of BN, RH, MM can be considered as peripheral compared to the other central females whose core areas fell 100% within the boundaries of the total male core area. There was no obvious relationship between the degree of overlap between individual female core areas and the core area of all males combined and an individual's position in the dominance hierarchy.

7.6 Discussion

The estimates of community range size during this study period are considerably larger than the previous estimates of approximately of 7km^2 by Newton-Fisher (1997). This may be due to slight differences in methodology, (Newton-Fisher recorded locations within 25m^2 blocks compared to the 100m^2 blocks of this study). However, calculations using the MCP methodology should be largely unaffected. Moreover, additional trails were cut through the forest and the process of habituation continued which will have aided the location and following of chimpanzees. This may have resulted in a more complete record of chimpanzee ranging. That said, during this study individuals of the Sonso community were observed to feed upon a fig tree, and subsequently crop raid, outside the forest in the nearby village of Nyakafunjo for the first time since studies on this community began. Chimpanzees from other communities had been observed to feed here in the past. This may provide evidence of a shift or expansion of community range size. It is the author's belief that despite there being times when contact with the chimpanzees was lost, the outlines of range size produced during this study may be considered as an accurate reflection of the habitual area used by the community during this study period.

Even when accounting for variation due to differences in methodologies, the community home range area of the Sonso community seems quite small compared to other study sites (see table 7.1). This is particularly evident when considering the number of independent individuals (Figs 7.7). These differences may be due to ecological differences in food availability and distribution. At Mahale, Hasegawa (1990) proposed that females have larger core areas compared to those at Gombe. He

also suggested that females travelled more widely when food is abundant. He suggests that both these observations are a response to larger food patches in Mahale compared to Gombe, and that when food is abundant the community remains cohesive, ranging together, which weakens the sex differences in the ranging patterns. In contrast, a chimpanzee community in Senegal was suggested to occupy such a large community range area due to the paucity of food resources in this comparatively arid area compared to Gombe (Baldwin et al., 1982). Unfortunately, detailed phenological data are not available from many sites. However, broad category generalisations and comparisons of the density of chimpanzees between the woodland habitats of Gombe and Mahale and the forested habitats of Kibale, Tai and Budongo, suggest that there is some evidence that food supply may greater in forested habitats than woodland/gallery forest habitats. However, the data from Tai are anomalous. This may be a result of demographic events. In at least two of the samples the population was undergoing a major mortality event (Boesch & Boesch-Achermann, 2000). It is also important to consider the influence of neighbouring communities on determining community range area. Boesch & Boesch-Achermann (2000) state that the variation in community range size over time is best explained by encounter risk with neighbouring communities. Territory size (community range) was found to be negatively related to encounter rate with neighbouring communities. In addition, in Tai forest there is a lot of human disturbance and logging activities (Boesch & Boesch-Achermann, 2000) which may be affecting the demography of the study community. Recent research on adjacent communities in the Tai Forest have shown that ranging patterns are affected by the presence of oestrous females in neighbouring communities (Herbinger & Boesch, 1997).

Until adjacent communities are habituated, it is impossible to know how the presence and size of neighbouring communities influence the territory size of the Sonso community. At least 2 other communities are believed to neighbour the Sonso community (see Chapter 2). Other factors which may be influencing the size of the Sonso community home range are the groves of *Brousonnetia* trees around the sawmill area. This species provided both fruit and young leaves as food resources for the chimpanzees and was fed upon during 19.87% of the total feeding observations.

This is an exotic species which was introduced to provide timber for the sawmill. It is now not used as the sawmill does not operate.

Analysis of the total area used by females compared to that used by male chimpanzees explicitly shows evidence of a bisexual community. Using all data collected the male range area totally overlaps that of the females. The male range area may be considered to be equal to the community range area. Looking only at core areas, defined as the area used in 80% of observation points, the core area used by all females is approximately 80% of the core area used by males and is located within the range area of the males. This provides strong evidence supporting the second model of chimpanzee dispersion proposed by Wrangham (1979b), that female range areas are distributed within the home area of the male chimpanzees. This supports previous arguments by Chapman & Wrangham, (1993), Pusey (1980), Kawanaka, (1984). At Mahale, females also used approximately 80% of the area used by males and the male home range was also estimated to approximate that of the community home range, (Hasegawa, 1990). At Mahale, four distinct categories of females were identified by the location of their ranges. It is suggested that these categories may be biased by females in the process of transferring from one community (K) to another (M). Uehara (1981) also argued that the differences in female ranging patterns at Mahale would be due to processes of immigration; newly transferred females using the boundary areas. Although, this may be the case in some instances, it was not observed during this study. In this study, the females which were identified as being peripheral were all adult females with offspring and classified as old by their characteristics of balding head and grey/brown backs. Clea (CL), who was seen to immigrate into the community during this study, could not be classified as peripheral. Not only did the range of the community males completely overlap that of the females, but there was considerable overlap, suggesting that females are avoiding boundary areas. This suggests that there may be a cost associated with having a core area located near these boundary areas. Chapman & Wrangham (1993) also found that females tended to avoid boundary areas of the community range. In addition in the Sonso community, the core area of the community range represented 10-30% of the total community range. Similarly,

Boesch and Boesch-Achermann (2000) state that the core area, where chimpanzees spent 75% of their time, represents only 32% of the community area. This suggests that both males and females associate boundary areas with danger. During this study one encounter and attack between the two communities was witnessed (see Chapter Two). Patrolling behaviour was observed by parties composed mainly of males and oestrous females. During a patrol the chimpanzees would silently leave a feeding tree and move purposefully towards a boundary area, stopping occasionally as if to listen and/or wait for other chimpanzees to join. It is unclear what would initiate a patrol. The incursions deep within another community's territory, as observed in Gombe (Wrangham & Peterson, 1996; Wrangham, 1999) or Tai (Boesch & Achermann-Boesch, 2000) were not observed during this study. However, observations suggest that the community boundaries of the Sonso community do overlap at least during periods of food scarcity (see Chapter 5). Therefore it seems reasonable to assume that there is some danger associated with being on the periphery of the community range. A female on the periphery of the community range presumably associates less with other males and females in the community. This could be costly in terms of maintaining social relationships, assessing mating opportunities and the social environment for the development of offspring. In this study, there was no link between a females' position in the dominance hierarchy and the location of a female's core area as either central or peripheral. It was old females which were identified as being peripheral. It is possible that during their lifetime they have already invested in social relationships which now do not need to be regularly maintained. It is also possible that their sons are now the top ranking males, and that this alone will allow reintegration into the group as and when the female chooses to join the main group. This will allow the peripheral females to experience reduced feeding competition by being on the edge of the community range perhaps without a substantial cost of lower social cohesion. However, the risks of infanticide by neighbouring community males should be the same regardless of the females age.

As in the study at Gombe (Wrangham & Smuts, 1980) and Kibale (Chapman & Wrangham, 1993), females were found to have core areas approximately half the size of male chimpanzees. The data in this study on male core area size is comparable

to that recorded by Newton-Fisher (1997). This, together with the agreement between different analyses, supports the accuracy of range size estimation. No significant differences in core area sizes were found between different age categories within the sexes. The major female life history trait influencing the size of core area was whether or not she was having reproductive cycles during the study period. There was a significant difference between the size of the core areas of females categorised as non-cycling and cycling. The estimation of an individual's core area of use from 80% of observations, as commonly used in other studies, was found to have biological meaning for the majority of females in the Sonso community. Examination of the utilisation plots of males did not show such distinct use of core areas. There are variations in the distinctiveness of the core areas between females. Generally, mothers with infants have more distinct core areas than cycling females. This suggests that when in oestrus or when cycling females leave their core area in order to associate with males. The percentage area of the individual total range which is considered to be the core area is considerably smaller than that used by chimpanzees in Gombe, (Gombe 40- 60% compared to 15-40% in this study), (Wrangham & Smuts 1980). The size of individual core areas found in this study was very similar to those found in Gombe (median females 2.1; males 4.1). It would appear that the core areas in the Sonso community must have a higher degree of overlap compared to those in the Kasekala community, Gombe, given the higher density of chimpanzees in the Sonso community. This is very interesting: the higher density of chimpanzees would imply a richer food supply, however this increased food supply does not seem to result in lower travel costs for females as indexed by range area. It is probably appropriate to assume that there are increased opportunities for association between individual females, given their higher density and high degree of overlap, which will be discussed in Chapter 8. The degree of overlap between female core areas was significantly less than that between male core areas, thus indicating that females are more dispersed in relation to one another than males. Wrangham (1986) estimated that a female's stable core area, where 80% of observations obtained over at least 8 days was less than 20% of the community range. The results for this study are in agreement, because the mean non-cycling

female core area size, using data points collected over a longer time span, was less than 15% of the community range.

Pusey et al. (1980) suggested that females may be competing for access to core areas. So far no studies have reported a relationship between a female's position in a dominance hierarchy and range area. Chapman & Wrangham (1993) found a positive relationship between male range size and dominance, however no relationship was found between a female's position in the hierarchy and range size. Newton-Fisher (1997) concluded that there was no relationship between the Sonso male core areas and dominance, although there were significant correlations between male status and total range area using MCP and cluster analyses. The results of the analyses of individual female core area size and position in the dominance hierarchy during this study were interesting. Although, due to small sample sizes, the results may only be considered as preliminary, they suggest that the relationship between dominance and core area size for adolescent females and adult females is different. The core area size for adult females appears to increase, (all r_s values are negative), with the female's position in the dominance hierarchy, whereas that of a adolescent female tends to decrease, (all r_s values are positive), with increasing rank. This difference may be due to the establishment of core areas by adolescent females. When a new female immigrates into a community initially, she may associate and range with the males of the community. She may use her sexual swelling as a 'social passport' enabling her to be tolerated as a member of the male groups (Boesch & Boesch-Achermann, 2000). As she establishes relationships with the females in the community she may establish a core area and then produce offspring. Adult females having established core areas and produced offspring experience different selection pressures. Group size is limited by food patch size and distribution; non-cycling females do not have a social passport to allow them to integrate into predominantly male groups and therefore may have to restrict their ranging patterns to smaller core areas. If access to either feeding patches or parties is through a process of contest competition the higher ranking females will have priority of access. This may result in high ranking adult females having larger core areas, as they suffer reduced feeding competition in relation to lower ranking females, and thus may increase travel costs.

It is assumed to be of benefit for females to associate in larger parties. The results from Chapter 5 show that when food availability and presumably travel costs were low, females chose to associate in mixed parties. The quality of the habitat within core areas was not assessed. However, due to the extensive overlapping nature of female core areas it is not expected to change very much between individual core areas. In addition, Newton-Fisher concluded that as a community and as individuals, male chimpanzees showed a clear preference for particular forest types, however there were no habitat differences between the core areas of individuals.

Descriptions of and comparisons between individual home range areas must remain preliminary until it is possible to follow all individuals as they range from night nest to night nest, sampling all party types and areas of the home range equally. This is especially true when considering the data collected for female chimpanzees, because the number of days that each individual was observed showed large variations. However, although these analyses are preliminary, they offer an insight into the behavioural diversity of ranging patterns both within and between the sexes. In summary, compared to data from other studies sites, in particularly Gombe, the density of chimpanzees at Budongo is higher. However, individual female core area sizes are similar to those of Gombe chimpanzees. This suggests that the female ranges must overlap more at Budongo and thus provide increased opportunity for females alliances; this is the subject of the following chapter.

7.7 Conclusions

- Overlap analyses of total male and female ranges provides evidence of a bisexual community.
- Within sex categories, there was no significant relationship between the size of core areas and age (adolescent vs. adult)
- Non-cycling females occupied core areas which were approximately 50% smaller than male core areas. Cycling females occupied core areas which were not significantly different from the size of male core areas.
- Patterns of home range utilisation, as indicated by the utilisation plots, show that compared to males, females have more distinct core areas.

- Male core areas overlap significantly more with each other than female core areas, indicating that female chimpanzees are more dispersed in relation to each other than male chimpanzees
- There is wide variation in the overlapping of individual female ranges by the total male community range allowing the identification of peripheral and central females.
- The relationship between the size of female core areas and dominance was complex. There is a possible relationship between the size of female core areas and dominance when estimated using the multi-core cluster analysis technique. However, this effect appears to be different for adults and adolescents. Adult females show an increase in core area size with rank whereas adolescent females show a decrease in core area size with increasing rank.
- There is no obvious relationship between the extent to which females are peripheral and dominance hierarchies. The peripheral females are all old. RH and BN both have dependent offspring. Interestingly, RH was observed to associate with the other community members frequently the month prior to giving birth to RS in the centre of the community range.
- The relative size of the Sonso community range is small compared to other study communities. This may be explained by there being a more concentrated or constant food supply in this area. When studying several communities there appears to be a relationship between relative community size and habitat.
- The density of chimpanzees in the Sonso community appears to be higher than the woodland/gallery forest dwelling chimpanzees at Mahale and Gombe. However, the size of individual core areas are very similar to those described at Gombe. Thus, the ranges of females in the Sonso community may be interpreted as being more overlapping in nature.

Chapter 8

Female Social Relationships

8.1 Introduction

Compared to our understanding of male social relationships our knowledge of female chimpanzee social relationships is less complete. This is probably a combined result of females in the wild spending more time alone, reducing the frequency of interactions and also because dominance interactions between females are usually less dramatic than those between males (Baker & Smuts, 1994). Yet, the understanding of female social relationships is crucial to understanding of adaptive significance of the chimpanzees' social system. According to Wrangham (1980), females of any species should be distributed in space in a manner which enables the most efficient exploitation of food resources. Males in turn should be expected to compete among themselves for access to females. This is an extension of the parental investment theory proposed by Trivers (1972), which states that females typically invest more in their offspring than males (exceptions being some monogamous species), and thus the limiting resource for the reproductive success of males is access to females. Females, on the other hand, maximise their reproductive potential by their investment in offspring, and thus should compete for access to food resources. Where forming alliances is beneficial to the defence of food resources, females are expected to form alliances with kin members, resulting in female-bonded groups. This is usually the case in social old world primates, where female-bonded groups with male dispersal is common. However, in chimpanzees, *P. troglodytes* and *P. paniscus*, it is invariably the females which are the dispersing sex.

It is expected that variation in the ecological conditions faced by different populations may result in variation of the relationships between females (Wrangham, 1980; van Schaik, 1989; Sterck et al. 1997). Attempts have been made to explain the differences observed between the social organisation of *P. troglodytes* and *P. paniscus* on the basis of differences in their environment (Wrangham, 1986, 1992;

Chapman et al., 1994 see chapter 5). As with other chapters of this thesis, this chapter will attempt to improve our knowledge of the extent of variability in behavioural traits within one species, *P. troglodytes*.

Female Life Histories

All studies of chimpanzee communities have found that females are the dispersing sex (Nishida, 1979, 1989; Pusey, 1979, 1980; Goodall, 1986; Boesch & Boesch-Achermann, 2000). However, the proportion of females transferring between communities varies between study communities, [Gombe 13%, Goodall (1986), or 50%, Pusey et al. (1997); Tai 95%, Boesch & Boesch-Achermann (2000); 87% Mahale, Nishida (1990)]. Females typically move between communities during late adolescence when they are exhibiting full sexual swellings and are thus attractive to males (Nishida, 1979; Pusey, 1980; Boesch & Boesch-Achermann, 2000). At Gombe, younger adolescent females have also been observed to transfer between communities (Pusey, 1979). Also at Gombe, females that ultimately remain in their natal community and raise offspring were recorded as being absent from the community during some periods. This raises the possibility of extra-community copulations without the costs involved in permanently transferring between communities. At Mahale, Tai and Gombe there were some adolescents which were observed to visit the study community but failed to fully integrate into the community. A female's decision to stay or leave a community will probably depend on a wide variety of factors including the relative sex ratio of hers and surrounding communities, and possibly her mother's rank. Pusey (1979) suggested that provisioning with bananas may have influenced a female's decision to stay or return to the natal community at Gombe. At Mahale, immigrant females were observed to return to their natal community in seasons when there was abundant fruit available in the natal community range (Hasegawa, 1989). There also appears to be some variation in the speed of integration into a new community. Boesch & Boesch-Achermann (2000) state that all immigrant females transferred rapidly and did not display the usual habituation problems associated with other females in the community; whereas integration into a new community at Gombe and Mahale may

be a more gradual process over months or years of visits (Goodall, 1986; Hasegawa, 1989). Generally, the available evidence suggests that females only transfer once during their lifetime. Only at Mahale have *adult* females been observed to transfer between communities. This may be considered an exceptional circumstance, as it was most likely the outcome of the disappearance of all the males in their original community (Nishida, 1979; 1990).

In *P. paniscus* females are also the dispersing sex (Kano, 1992). Again, females transfer between communities during adolescence and establish themselves in neighbouring community ranges. These adolescent females slowly establish bonds one at a time with females in their new community, and gradually become central figures in the community (Furuichi, 1989).

Female dispersal is usually considered to be an evolutionarily adaptive strategy to avoid inbreeding. However, as mentioned earlier, the problems of inbreeding could be avoided by temporary transfers to neighbouring communities without the risk and cost of emigration. Perhaps other social decisions which could affect future reproductive success may also be important in the decision to transfer. Boesch & Boesch (2000) provide evidence to support this argument, stating that more females immigrated into the Tai community when the number of community males was high compared to when the number of males was low. The number of males in a community may be important to a female, offering more mate choice and also increased safety from infanticidal attacks by other community males, and, perhaps due to inter-community competition, more secure access to food resources.

Generally, adolescent females show sexual swellings when they transfer from one community to another. However, they also experience a period of reproductive sterility. The selective advantage of a long period of adolescent sterility may be to allow females time to investigate new communities, select suitable mates and form new relationships (Pusey, 1980; Goodall, 1986). The swellings may also be used as a 'social passport' allowing easier integration into the new community (Boesch & Boesch-Achermann, 2000). Once fully integrated into the community the female will then conceive. It is possible that this period of integration into the community, and thus period of reproductive sterility, will be longer in immigrant females than

adolescent females which remain in their natal community. Thus, this may be one benefit to a adolescent female of remaining in her natal community.

Female Association Patterns

The information on female association patterns that is available from both the wild and captive situation is inconsistent. In all communities studied, male-male bonds are consistently stronger than male-female and female-female bonds (Nishida, 1979; Ghiglieri, 1984; Goodall, 1986; Wrangham et al., 1992; Boesch & Boesch-Achermann, 2000). However, there are inconsistencies in the strength of bonds both between the sexes and between females. Boesch & Boesch-Achermann, (2000) compare the data on dyadic association indices, (DAIs), between the sexes from four different communities (Mahale, Gombe, Kibale and Tai). At Tai Forest, the average association between females is higher than at other sites. They conclude that Tai chimpanzees form larger parties which include more members of both sexes. However, caution is essential when comparing association indices between sites due to differences in data collection. For example, at Tai, the main focus of data collection was on nut cracking and hunting behaviour, activities which generally attract many party members. Doran (1997), studying the same chimpanzees during a period of food scarcity, concluded that the party size and association patterns of the Tai chimpanzees were similar to those of East African chimpanzees. However, comparisons of association indices within sites are possible. What is interesting is the distribution of association indices between females within the Tai community (Boesch & Boesch-Achermann, 2000). Although, as a community, female-female association was lower than that between the males, certain dyads of females had association indices higher than any of those between males. In fact, the highest of all DAIs were between adult females with three dyads spending respectively 66%, 71% and 79% of their time together. These values were within the range of association between mothers and adolescent offspring. They were also stable female associations which lasted at least four years and were only disrupted by the death of their partners. The females were judged to be of similar age and therefore not sisters. They were also of similar rank (although data on female dominance hierarchies is not

presented). These close female-female associates are described as 'friends', observed to frequently share food and support each other in conflict situations. Surprisingly, they were not observed to be frequent grooming partners. These females with long lasting alliances were stated to also hold the highest rank positions in the female dominance hierarchy. At other study sites no such strong associations between individual female dyads have been reported.

At Gombe, Mahale and Kibale, female-female association is less common than that between males and females, which in turn is less common than that between males (Nishida 1979; Goodall, 1986; Wrangham et al. 1992). In contrast, other studies at Kibale and Bossou have suggested that females show greater affiliation to each other than they do to members of the opposite sex (Ghiglieri, 1984; Sugiyama & Koman 1988). Wrangham et al. (1992) suggested that the differences between the results of the two studies in Kibale may have been as a result of differences in habituation levels; less habituated chimpanzees would result in the over-estimation of the importance of mixed parties. It has been suggested that the social organisation of the chimpanzees at Bossou may have been influenced by the disturbed habitat in which they are living, which has resulted in the population becoming isolated (Sugiyama, 1988). Under such conditions adolescent females may remain in their natal community.

Boesch & Boesch-Achermann, (2000) suggest that the stronger female-female bonding in Tai chimpanzees is a result of both the community size and sex ratio, leading to large mixed parties which contain a large proportion of the individuals in the community. This higher social cohesion in turn results in increased competition amongst females, which leads to a situation where it becomes adaptive for females to forge long-term alliances. They support this theory by stating that when the density of chimpanzees in the study area decreased females probably faced less female-female competition and generally the DAIs between females decreased. At Gombe, Mahale and Kibale, female chimpanzees associate less, which Boeasch & Boesch-Achermann (2000) suggest, decreases female-female competition in the community and thus the need for females to form coalitions.

The stage in the life history of a female is also likely to affect her association patterns. For the first few months following transfer, immigrant females often travel with males, even when not in oestrus, and only associate with females when males were also present (Pusey, 1979; Boesch & Boesch-Achermann, 2000). Goodall (1986) comments that the changing nature of a female's life history, reproductive cycle and family structures, and that of her companions, will affect the nature of her relationships with other chimpanzees. A comparison of the relationships of a brother, *Figan*, and sister, *Fifi*, with other chimpanzees showed that *Fifi* spent far less time with even her closest female companions than *Figan* did with other males. In addition, there was less consistency from year to year in *Fifi's* choice of associates reflecting her continually changing life history. A number of friendly relationships between adult females are disrupted when the son of one reaches adolescence and attempts to dominate his mother's friend. If the latter threatens or attacks him, his mother will typically support him, and the lower ranking female may then start to avoid her former companion (Goodall, 1986).

In captivity, females have been described as playing a central role in the chimpanzee community (de Waal, 1982). Three sub-groups of females were recognised within the Arnhem community. The females in these sub-groups looked after each other's offspring and provided coalition partners during conflicts (de Waal, 1984). In contrast, when the dominance hierarchy of the males was unstable, a male would use any individual which would support his cause as an alliance partner. Baker & Smuts (1994) observed the formation of social relationships in another captive group of females, and concluded that females may also form opportunistic alliances when the female dominance hierarchy is unstable, such as during the formation of a new group.

In summary, all studies have demonstrated the close bonds between male chimpanzees, but the degree and nature of female relationships are far more variable. At least in captivity, and also at one site in the wild, Tai Forest, females form close association patterns similar in form to those between males (de Waal, 1982; Baker & Smuts, 1994; Boesch & Boesch-Achermann, 2000); whereas all other studies in the wild have suggested that females are more solitary by nature. Further studies of

female relationships in different study communities will help to elucidate the behavioural flexibility and the conditions under which females will or will not form alliances.

Female Dominance Hierarchy

In all communities of *P. troglodytes* studied to date males have been described as being dominant to all females in the community. However, the importance assigned to female dominance interactions in a community varies between studies. The usual situation appears to be for female dominance interactions to occur at a much lower frequency than male dominance interactions (de Waal, 1982; Goodall, 1986). However, within these same communities there are times of 'dominance striving' behaviour (de Waal, 1982; Goodall, 1986; Nishida, 1989), and at Kibale, dominance interactions between females occurred with the same frequency as those between males (Wrangham et al., 1992).

De Waal (1982) describes two different measures for the assessment of dominance relationships within a community: *real* and *formal* dominance. *Real* dominance is the sum total of all aggressive interactions. The outcome of such encounters is not totally predictable, particularly since chimpanzees have the tendency to form coalitions. *Formal* dominance is acknowledged in the greeting behaviour of chimpanzees known as the 'pant grunt'. It is a consistently reliable measure of the established dominance relationships. It is the only common form of social behaviour which is non-mutual: in other words if A pant grunts to B during a certain period, B will never pant grunt to A during the same period. Generally, formal and real dominance ranks will overlap. It is unclear when the formal dominance ranks will change, probably after the dominant individual loses a significant number of real interactions or the breakdown of a coalition. De Waal (1982) described the female dominance hierarchy as being based upon respect from below rather than intimidation and a show of strength from above. Antagonistic interactions were not found to be a good predictor of female-female dominance relations in either Arnhem or Gombe (Bygott, 1979; de Waal, 1982). Furthermore, at Arnhem 'greetings' or pant-grunt interactions were more common than antagonistic

interactions. De Waal (1982) suggested that female rank was based on individual age and personality and that the female dominance hierarchy was considerably more stable than that of males. In addition, de Waal, (1982) recognised a third type of dominance in which females may be dominant to males. Females may be dominant to males in 81% of interactions involving moving objects and choice of places to sit. This is interpreted as being a case of male deference, perhaps in an attempt by the males to win the favour and support of females for future conflicts.

Baker and Smuts (1994) analysed the dominance relationships in two captive groups and suggested a model of chimpanzee dominance. They compared the nature of female-female relationships and interactions during the formation of a captive group, a period when relationships may be considered unstable, with those of a stable group. They concluded that when forming new relationships, female chimpanzees will use competitive strategies similar to those well documented for males. In particular, the frequency of reconciliation, alliance formation and agonistic dominance interactions with no apparent context other than a drive for status, all increased. They compared the situation to the life history of wild chimpanzees and suggest that for females the drive for dominance is important when setting up core areas, after which the returns for increasing dominance are limited, whereas for males the pay offs for increasing an individual's dominance position are always high.

Recent analyses of 35 years of data from Gombe have revealed that dominance is an important component of female reproductive success (Pusey et al., 1997). High-ranking females had significantly higher infant survival, faster maturing daughters, and more rapid production of young. The authors suggest that given the foraging nature of female chimpanzees, higher rank probably influences reproductive success by helping females establish and maintain access to good foraging areas rather than by sparing them from aggression. High rank may confer better access to food, both by enabling a female to acquire and maintain a core area of high quality and by affording her priority of access to food in overlap areas.

In the wild, immigrant females face a considerable amount of aggression from resident females, as they transfer into a new community (Pusey, 1979; Nishida, 1989; Boesch-Boesch-Achermann, 2000). Pusey (1980) acknowledges that

interactions between newly immigrated and resident females are rare; however, 7 out of 8 females which immigrated in to the community were observed to be attacked by resident females, and 4 of these attacks were by coalitions of females. Each time the attack was stopped by male intervention. At Tai, it is believed that when transferring between communities, immigrant females face less aggression from resident females than that reported from other sites (Boesch & Boesch-Achermann, 2000). Nishida (1989) documented the transfer of both adult and adolescent females from one community (K group) to another community (M group) following the disintegration of K group. Even six years following the transfer, there was still a divide whereby ex -K group females tended to associate together and likewise with the M group females. M group females had more central ranges and the K group females continued to associate in the northern part of the range. Nishida also recorded dominance interactions and found that younger, nulliparous and short-tenured females tended to pant-grunt to older, multi-parous and longer-tenured females. He noticed that females tended to compete with those of like age when young, but that they avoided aggression when older. This agrees with the hypothesis of female dominance behaviour suggested by Baker & Smuts (1994). The long-term female coalitions documented in the Arnhem colony may be explained by the constant availability of allies. Nishida (1989) suggests that as female aggression in the wild is infrequent, the female coalition is opportunistic. Aggression by resident females may indirectly affect the reproductive success of immigrant females, by delaying the establishment of core areas and the peripheralisation of core areas (Nishida, 1989).

Furuichi (1989) found that in *P.paniscus* the oldest females were the most dominant and adolescent females received aggression from resident females. Bonobo females are often dominant to males and form close association with males and other females. Perhaps as a result of increased female sociality, females are able to form coalitions and dominate males. However, Stanford (1998) suggests that if social dominance is considered as distinct from feeding priority then the dominance relationships between bonobos and chimpanzees are similar. This is because of observations by Wood & White, (1996, cited in Stanford 1998) who found that the

majority of female dominated interactions occurred during feeding and could therefore be interpreted as male deference, resulting in female feeding priority.

8.2 Aims

The purpose of this chapter is to describe the female social relationships for another community of forest living chimpanzees, in order to increase our understanding of the behavioural diversity in female chimpanzees and to address issues about the ecological influences on social structure. The choice of association partner is assumed to represent a decision based upon the costs and benefits of associating with other individuals or remaining alone. The following aspects of female behaviour will be investigated:

- The nature of female dominance relationships. A dominance hierarchy will be established based on pant grunts and agonistic interactions. This dominance hierarchy was used in Chapter 7 to compare ranging patterns and to address the question of how female dominance influences resource competition.
- General association patterns of the sexes within the community and detailed association patterns between individuals.
- The effect of changes in food availability on the association patterns within the community.

6.3 Methodology

Dominance Behaviour

Dominance interactions between females were recorded both during focal sampling and *ad lib* data collection throughout the study period (June 1997 - December 1998) by both myself and Geresomu. As the majority of observations were in feeding trees, the context of all interactions may loosely be defined as feeding. The behaviour of the dominant and subordinate individual was recorded in as much detail as possible. this allowed five different dominance behaviours to be identified as follows:

Aggression: this included all physical threats (e.g. the raising of an arm) and actual physical contact between individuals. The dominant individual is interpreted as the individual who either moves away or emits a pant grunt.

Chase: this included all aggressive interactions which resulted in one individual chasing another. The dominant individual is interpreted as the individual chasing.

Displace: this behaviour was the result of the one individual moving away as another individual approaches, with no obvious sign of threat from the approaching individual. The dominant individual is interpreted as the individual approaching from which the subordinate moves away.

Insert Finger in Vagina: this indication of relative dominance ranks occurred more frequently during dominance interactions between males and females. The dominant individual inserts a finger in the vagina of the subordinate. Rather than overt competition, this appeared more like a gesture to reaffirm dominance relations.

Pant-grunts: this is a soft vocalisation directed from one individual to another. The dominant individual is interpreted as the individual to whom the pant grunt is directed. This was the most common form of the recognition of relative dominance between two individuals. This was a common behaviour of females towards any adult male. On these occasions it was difficult to assess precisely who the subordinate female was pant-grunting to, and this was exacerbated by the presence of males.

In order to construct a dominance hierarchy, two matrices were derived. One which used only pant grunt data, representing *Formal* dominance and the other which included all other dominance behaviours which may be considered to represent *Real* dominance (Noe et al., 1980; de Waal, 1982). Individuals were arranged in the matrix so that the dominant individual, (who was never supplanted), was at the top of the matrix. The other individuals were arranged in order so that the minimum number of supplants appears on the left hand side of the diagonal. Due to the high proportion of missing values for dyads for which no dominance interactions were observed some dominance relationships remained ambiguous, and further statistical analyses of the dominance hierarchies was not pursued.

Association patterns.

Group composition data, including all independent individuals, were collected every 15min. As in Chapter 5, only independent scan data were used (N=3095), that is only consecutive scans which included a change in party membership were included. Association indices were calculated using a *twice weighted* association index (Martin & Bateson, 1986). All scores are distributed between 0 (no association) and 1 (complete association).

$$DAI = c/(a+b+c),$$

where a = the number of associations containing individual a without b,
b = the number of associations containing individual b without a,
c = the number of associations containing a and b.

This index is commonly used in studies of chimpanzee associations (Ghiglieri 1984; Wrangham et al. 1992; Newton-Fisher, 1997) as it is recommended by Cairns & Schwager (1987) for use in situations where individuals are commonly found together. Mean DAI's were calculated for female-female, male-male, and male-female dyads for comparison with other sites.

In order to investigate the effect of changes in resource availability on association patterns, association patterns were analysed from two separate periods of varying food availability. These periods were chosen as the periods of most and least food availability (see Chapter 4). A '*food rich*' period occurred during the five phenology periods between and including Feb(2) and Apr(2); and a corresponding '*food poor*' period was defined between and including the five phenology periods Jun(1) and Aug(1). The total number of scans during the '*food rich*' period was 613 and during the '*food poor*' period 320. Again mean DAI's for male-male, female-female and male-female dyads during each period were calculated. Comparisons were made between the different sex and life history categories: adult and adolescent males and adult and adolescent females; adult and adolescent males and cycling and non-cycling females. Again, cycling females were classified as those females that had shown a full sexual swelling at any time during the whole study period.

8.4 Analyses

The multi-variate statistical technique, cluster analysis, was used to describe the association patterns between individuals in the community. This was performed in Minitab version 12. The results of the twice-weighted association indices were entered as a distance matrix and the average linkage method used to determine how the distance between two clusters is defined. The cluster analysis performs groupings based on the distance between values for individuals in the matrix, the smaller the value for a dyad the closer the association, therefore since the association indices produce values where the higher the value the greater the association these values where transformed by the equation 1/x, where x = the dyadic association index. The procedure uses an agglomorative hierarchical method that begins with all observations being separate, each forming its own cluster. The two closest clusters are then joined together, with further clusters either joining the original cluster or forming new clusters depending upon the distance between clusters. This process continues until all the clusters are joined as one. It is possible to determine how many groups are logical for the data set. For these analyses of associations the final grouping was always 1, equalling the entire chimpanzee community.

In addition, the non-parametric Kruskal -Wallis statistical test was used to test for differences in the association patterns of different sex and life history categories. The non-parametric Mann-Whitney test was used to compare association indices between the different food availability periods.

8.4 Results

Female Dominance Hierarchies

A total of 102 dominance interactions were recorded between females in the following categories: aggression N=9, chase N=10, Displace N=17, Insert finger in vagina N=2, Pant grunt N=64. The majority of these interactions were pant grunts, which may be interpreted as reconfirmation of relative dominance, rather than as potential contests for or challenges to dominance rank. Dominance interactions of both the lumped behavioural category of agonistic behaviour and those of pant grunts

could be arranged into a matrix to show a linear hierarchy. These two matrices were then merged together so as to produce an overall dominance hierarchy, without changing the rank positions of any individuals. However, extreme caution should be taken when considering this matrix to show the existence of a linear hierarchy (see Appleby, 1983). Due to the large number of missing values for dyads it is not possible to ascertain the real existence of a linear hierarchy. Martin & Bateson (1986) discuss the probability of a linear dominance hierarchy being an artefact of data analysis. That said, it is possible to see that females are clearly competing and the fact that no reversals of rank occurred in the 102 interactions suggests that the hierarchy is fixed. An alpha female, Nambi (NB) clearly emerged. Nambi both dominates the most individuals, (N= 11), and is the dominant individual in more interactions than any other female, (N= 27). In addition, Nambi was not observed to be supplanted by any other female. The latter criterion is often an indication of the most dominant individual, however, in this case further evidence was required due to the large number of dyads between which no dominance interactions were observed, and thus the dominance relationships remained ambiguous. General field observations also suggested that Nambi could be the alpha female, for example she was often in association with males, and could be seen in any area of the home range

From the dominance matrix it is also obvious that Clea, (CL), the most recently immigrated adolescent female, is the subordinate individual in the largest number of interactions and dominates no other individual, and is therefore very low ranking. It is clear that she is participating in dominance interactions with both resident adult females and other immigrant adolescent females. It is also evident that Kewaya, KY, who is now known to have stayed in the community to raise her first offspring, is involved in agonistic interactions with the resident adult and immigrant females of the community.

Table 8.1 Dominance Hierarchy By Pant Grunts (adult females, bold; adolescent female, italics).

	NB	**KG**	**KU**	**ZM**	**KW**	**RH**	**KL**	**BN**	**MM**	**RD**	**ZA**	**HT**	*KY*	*JN*	*SR*	*MK*	*CL*	*MH*	*VT*	*EM*	Tot
NB	-	2	3					1	1		2			3	1		4			1	18
KG		-	2											1	1		1				5
KU			-														1				1
ZM				-	1									1			2				4
KW					-						1		1			1	5	2		1	11
RH						-															0
KL							-														0
BN								-	1					1							2
MM									-												0
RD										-										1	1
ZA											-						1				1
HT												-									0
KY													-		1		3	2		1	7
JN														-			6				6
SR															-		4				4
MK																-	4				4
CL																	-				0
MH																		-			0
VT																			-		0
EM																				-	0
Tot	0	2	5	0	1	0	0	1	2	0	3	0	1	6	3	1	31	4	0	4	64

Table 8.2 Dominance Hierarchy By Agonistic Interactions (adult females, bold; adolescent female, italics).

	NB	**KG**	**KU**	**ZM**	**KW**	**RH**	**KL**	**BN**	**MM**	**RD**	**ZA**	**HT**	*KY*	*JN*	*SR*	*MK*	*CL*	*VT*	*MH*	*EM*	Tot
NB	-		1				3						2	2	1						9
KG		-								1				1							2
KU			-				1														1
ZM				-			1				2										3
KW					-								5				3				8
RH						-	1	1									1				3
KL							-														0
BN								-													0
MM									-												0
RD										-	1										1
ZA											-										0
HT												-									0
KY													-		1		4				5
JN														-	1		4				5
SR															-		1				1
MK																-					0
CL																	-				0
VT																		-			0
MH																			-		0
EM																				-	0
Tot	0	0	1	0	0	0	6	1	0	1	3	0	7	3	3	0	13	0	0	0	38

Table 8.3 Overall Dominance Hierarchy (adult females, bold; adolescent female, italics).

	NB	**KG**	**KU**	**ZM**	**KW**	**RH**	**KL**	**BN**	**MM**	**RD**	**ZA**	**HT**	*KY*	*JN*	*SR*	*MK*	*CL*	*VT*	*MH*	*EM*	Tot
NB	-	2	4				3	1	1		2		2	5	2		4			1	27
KG		-	2							1				2	1		1				7
KU			-				1										1				2
ZM				-	1		1				2			1			2				7
KW					-						1		6			1	8		2	1	19
RH						-	1	1									1				3
KL							-														0
BN								-	1					1							2
MM									-												0
RD										-	1									1	2
ZA											-						1				1
HT												-									0
KY													-		2		7		2	1	12
JN														-	1		10				11
SR															-		5				5
MK																-	4				4
CL																	-				0
VT																		-			0
MH																			-		0
EM																				-	0
Tot	0	2	6	0	1	0	6	2	2	1	6	0	8	9	6	1	44	0	4	4	102

Association Patterns

The association patterns of the whole community throughout January 1998-December 1998 are shown in Fig 8.1 (all indices are shown in a matrix in Appendix E.1). The y axis 'distance' represents the difference between the strengths of association between dyads. It is clear that generally similar levels of association join most members of the community, with the females Emma (EM), Ruda (RD), Banura (BN), Mama (MM), Harriet (HT) being much more 'loosely' associated with the community. Further examination of the association patterns within each sex category (Fig 8.2 & 8.3) shows more differentiation and variation between the association patterns of females compared to those of the males, even though the standard error between different categories is the same.

Table 8.4 Mean Dyadic Association Indices.

Dyad	N	Mean	Median	St Dev	SE mean	Min	Max
male-male	120	0.143	0.144	0.028	0.003	0.071	0.205
male-female	153	0.082	0.084	0.042	0.003	0.005	0.189
female-female	288	0.090	0.093	0.042	0.003	0.004	0.195

Fig 8.1 Dendrogram Showing The Association Patterns Of The Sonso Community During The Period January - December 1998

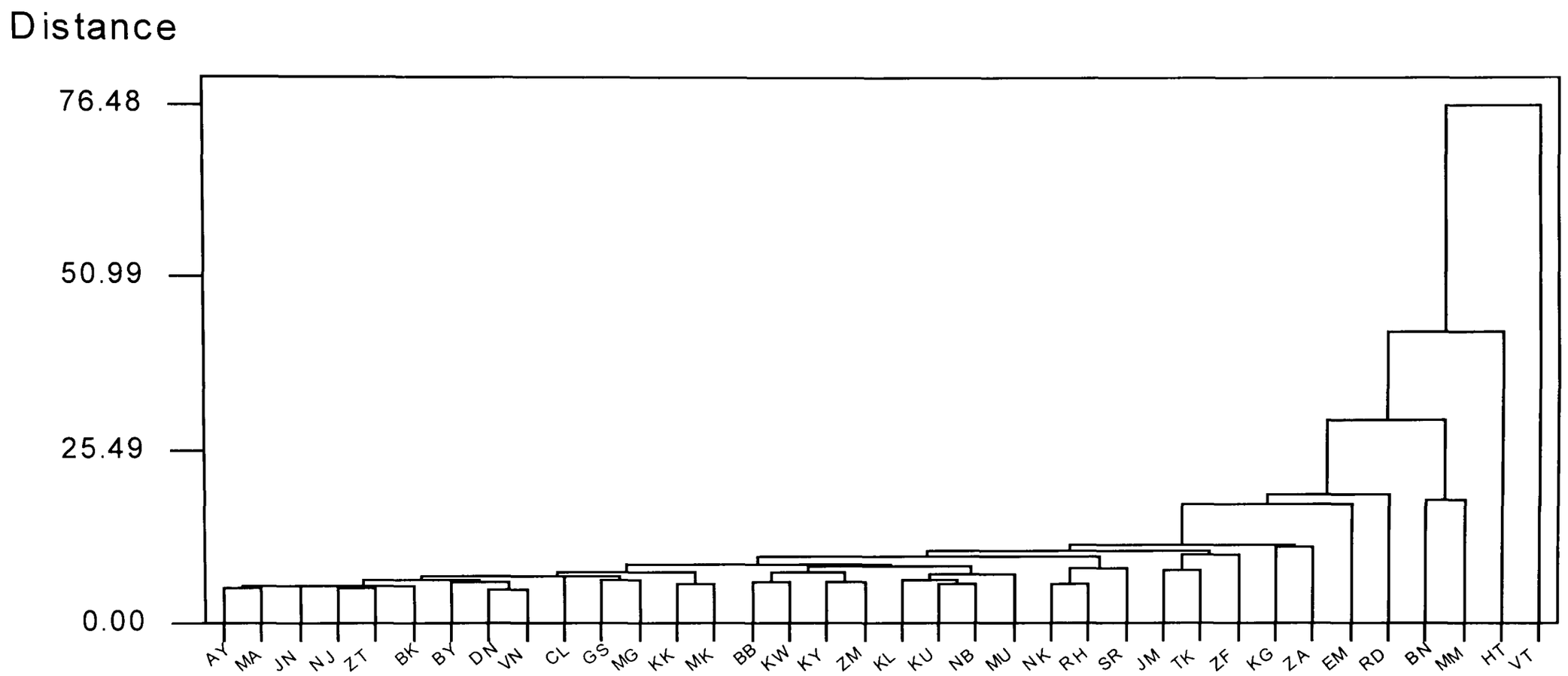


Fig 8.2 Dendrogram Showing The Association Patterns Of Females During The Period January - December 1998

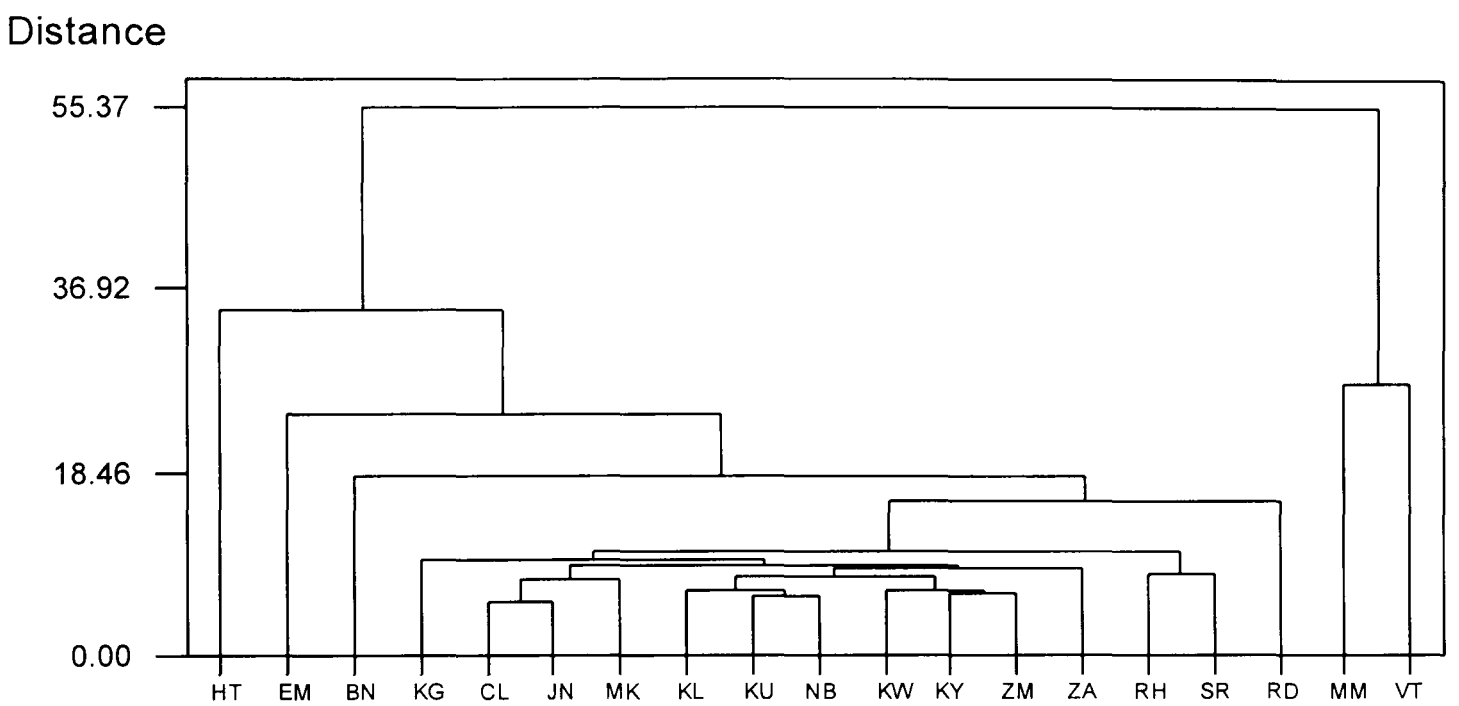
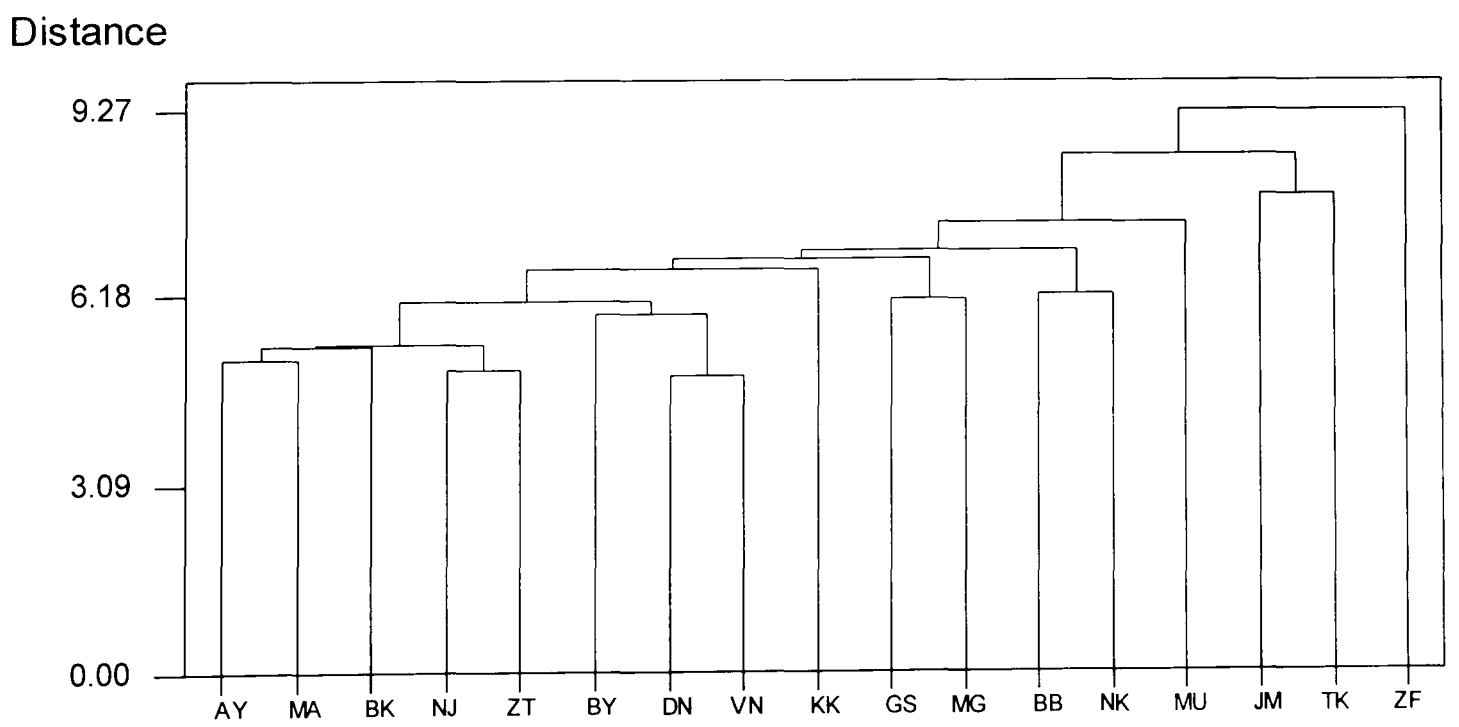


Fig 8.3 Dendrogram Showing The Association Patterns Of The Males During The Period January - December 1998



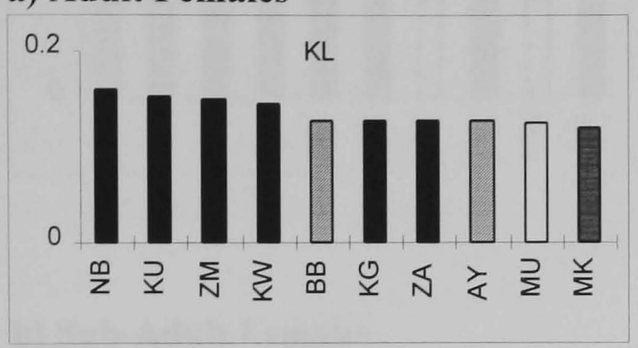
A Kruskal-Wallis test was used to test for a significant difference between the median dyadic associations indices (DAIs) of different sex categories (H=143.62, df 2, p<0.0001). Further Mann-Whitney tests between individual categories showed the median DAIs between males to be stronger than those between females (W=14006.0, p<0.0001), and also those between males and
females (W=36279.0, p<0.0001). However, there was no significant difference between those of females and those between males and females (W=31662.5, ns).

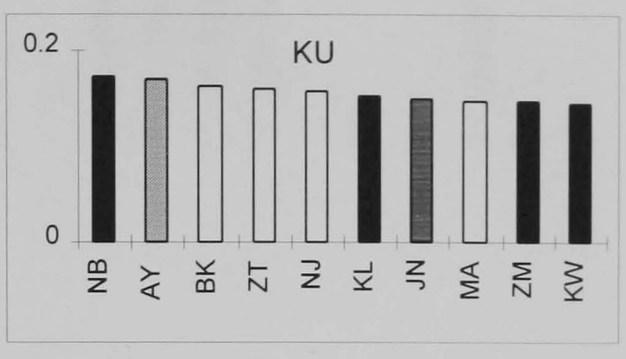
Even though overall female DAIs are less than those of males there were five dyads of females with association indices greater than the mean male-male index. These were Janie (JN) and Clea (Cl) DAI = 0.19; Kutu (KU) and Nambi (NB) DAI = 0.17; Kewaya (KY) and Zimba (ZM) DAI = 0.17; Kalema (KL) and Kutu (KU) DAI = 0.15 and Kwera (KW) and Kewaya (KY) DAI = 0.15. Within male-male dyads there were six dyads with DAIs greater than the mean. This shows that although generally female-female bonds are weaker than those between males, at least some female-female dyads have association strengths which are similar to those between males, and that the lower female-female associations strengths overall are probably a result of some of the females having considerably looser associations.

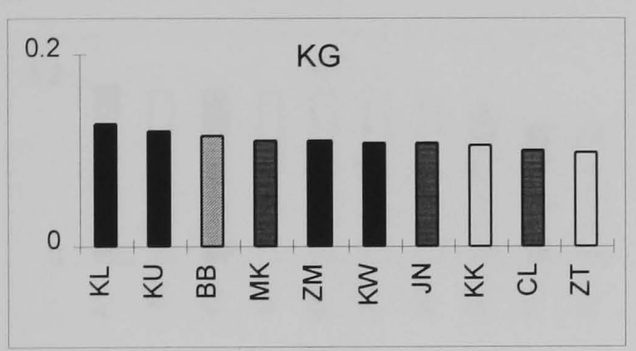
In order to describe the association patterns of different female individuals, bar charts were drawn showing the association indices of each female and her 10 closest associates (Fig 8.4). These charts show that in general the close associates of adult females are other adult females. The exceptions are Nambi (NB), whose closest associates include her adolescent son Andy (AY), her adult son Muga (Mu) and the alpha male Duane (DN); and Kutu (KU), whose closest associate is Nambi (NB) and adult males. The close association of KU and adult males is probably a result of her showing sexual swellings during the study. With the exception of Kigere (KG) and Mama (MM) no other adult females were cycling during the study period. In contrast, the close associates of adolescent females generally include more adult and adolescent males than those of the adult females. The exceptions were Vita (VT) and Kewaya (KY). The two closest associates of Kewaya were female, Zimba (ZM) her mother and Kwera (KW). Vita did not have any males as her close associates, this was probably because she did not exhibit full sexual swellings.

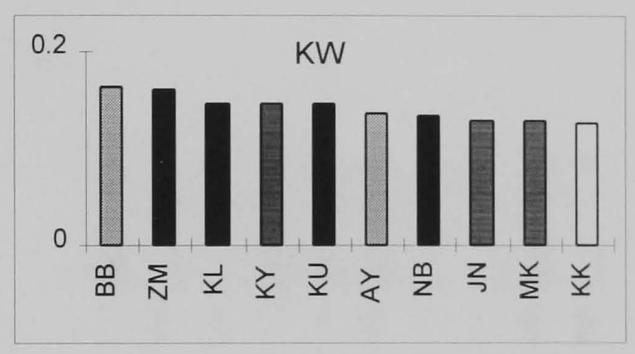
Fig 8.4 Bar Charts Showing The Closest Associates Of Individual Females. Solid black=adult female, striped black=sub-adult female, open=adult male and grey spots=sub-adult male.

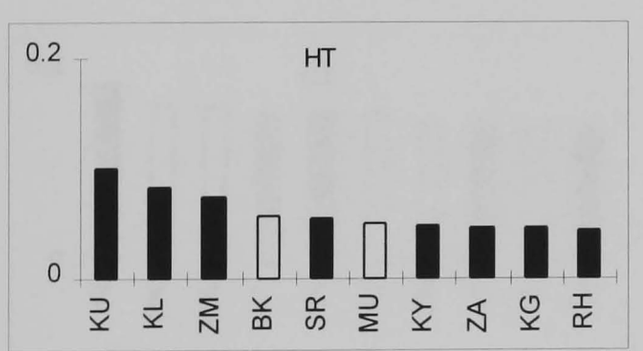
a) Adult Females

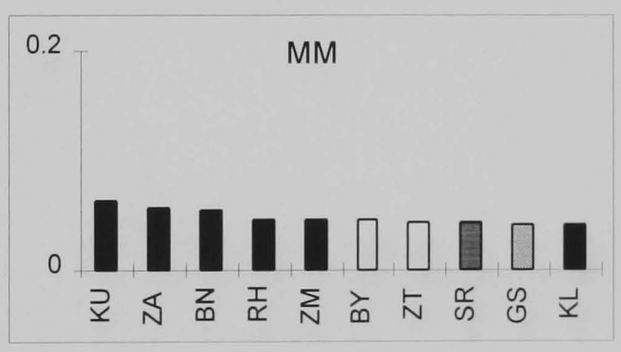


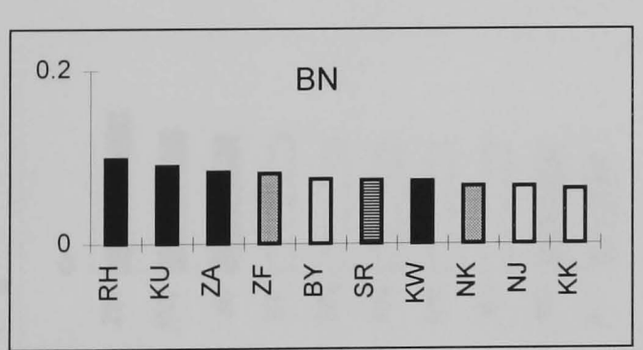


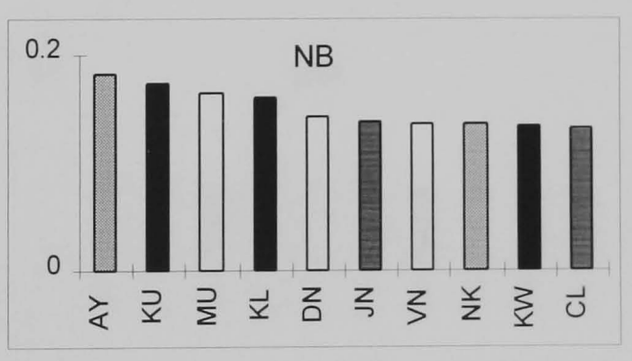


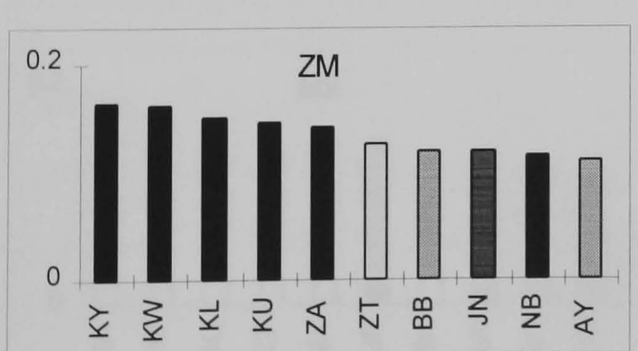


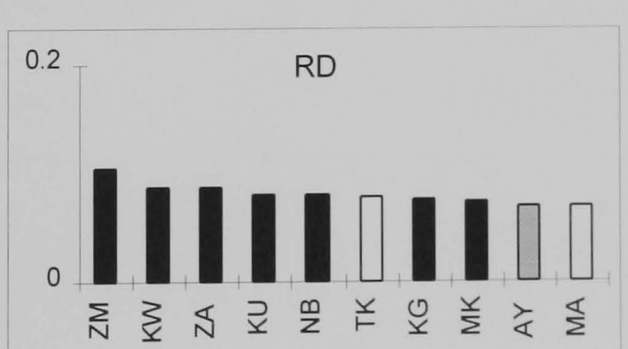


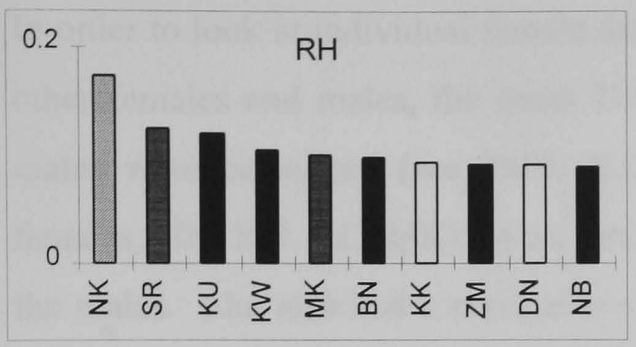


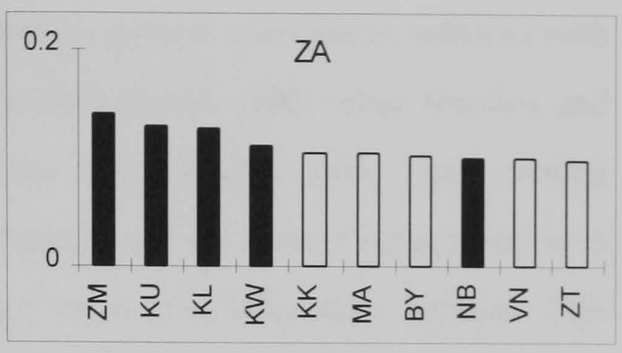




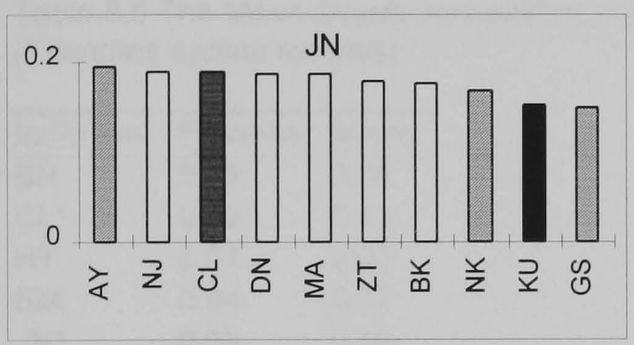


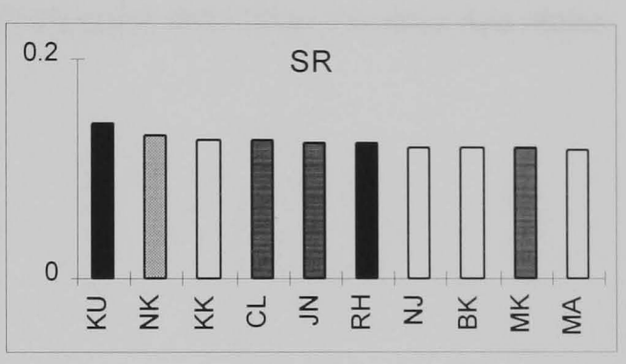


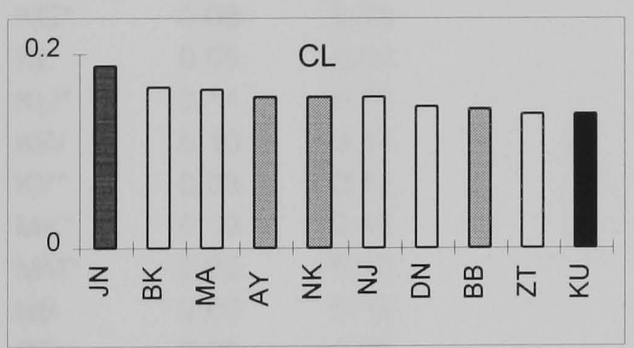


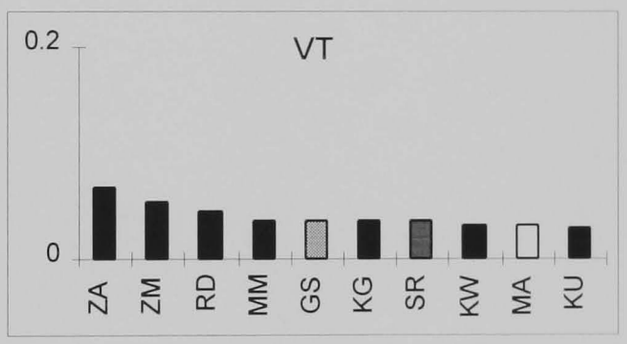


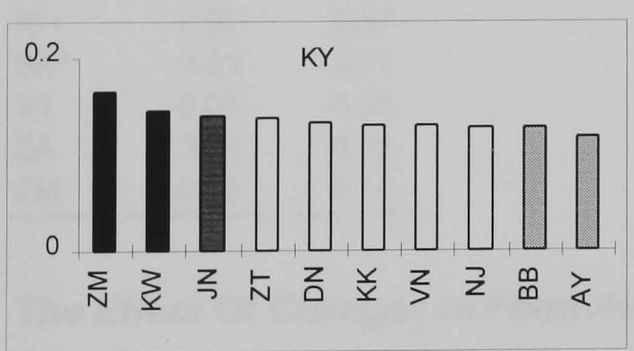
b) Sub-Adult Females

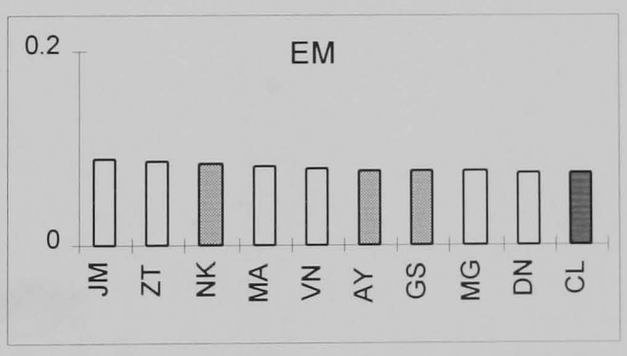


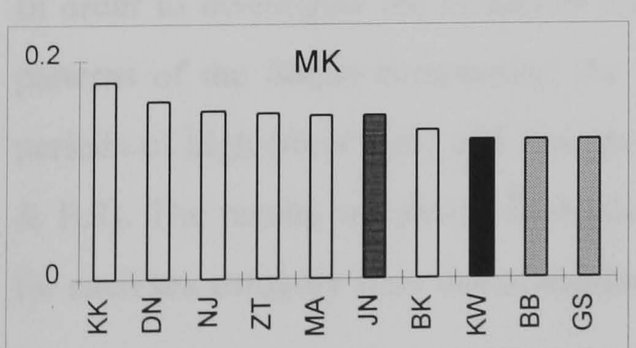












In order to look at individual female differences in general association patterns with other females and males, the mean DAIs for each female with other females and males were calculated (see Table 8.5). These revealed that aside from cycling females, (JN, KU, CL, MK), of all females, Nambi had the closest association with the males. She also had a comparatively high mean DAI with other females. This suggests that a possible benefit of high rank for females is greater association with the males of the community.

Table 8.5 The Mean Dyadic Association Indices Of Females With Other Females And Males (* denotes cycling females)

Individual	Females	Males
BN	0.05	0.05
CL*	0.09	0.13
HT	0.04	0.03
EM	0.04	0.07
JN*	0.09	0.16
KG*	0.08	0.08
KL	0.09	0.09
KU*	0.11	0.14
KW	0.10	0.11
KY*	0.08	0.11
MK*	0.09	0.13
MM*	0.03	0.03
NB	0.09	0.12
RD	0.06	0.05
RH	0.07	0.07
SR*	0.09	0.11
VT	0.03	0.02
ZA	0.09	0.08
ZM	0.10	0.10

The Effect Of Changes In Food Availability.

In order to investigate the effects of changes in food availability on the association patterns of the Sonso community, the DAIs for each dyad were calculated during periods of high (*food rich*) and low (*food poor*) food availability (see Appendix E.2 & E.3). The results are shown in dendrograms, Fig 8.5-8.10. Again the mean DAIs for each sex category were calculated (see Table 8.6 & 8.7).

Fig 8.5 Dendrogram Showing The Association Patterns Of The Sonso Community During The *FOOD RICH* Period.

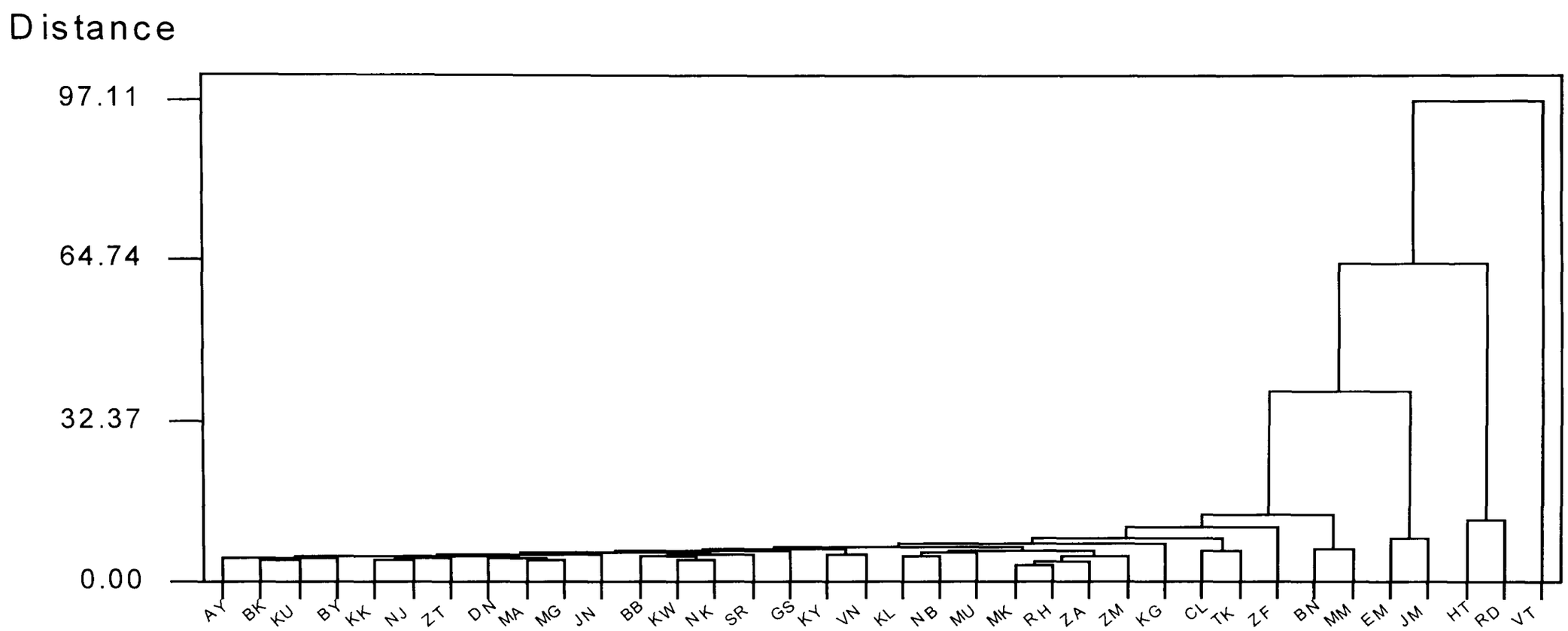


Fig 8.6 Dendrogram Showing The Female Association Patterns During *FOOD RICH* Periods.

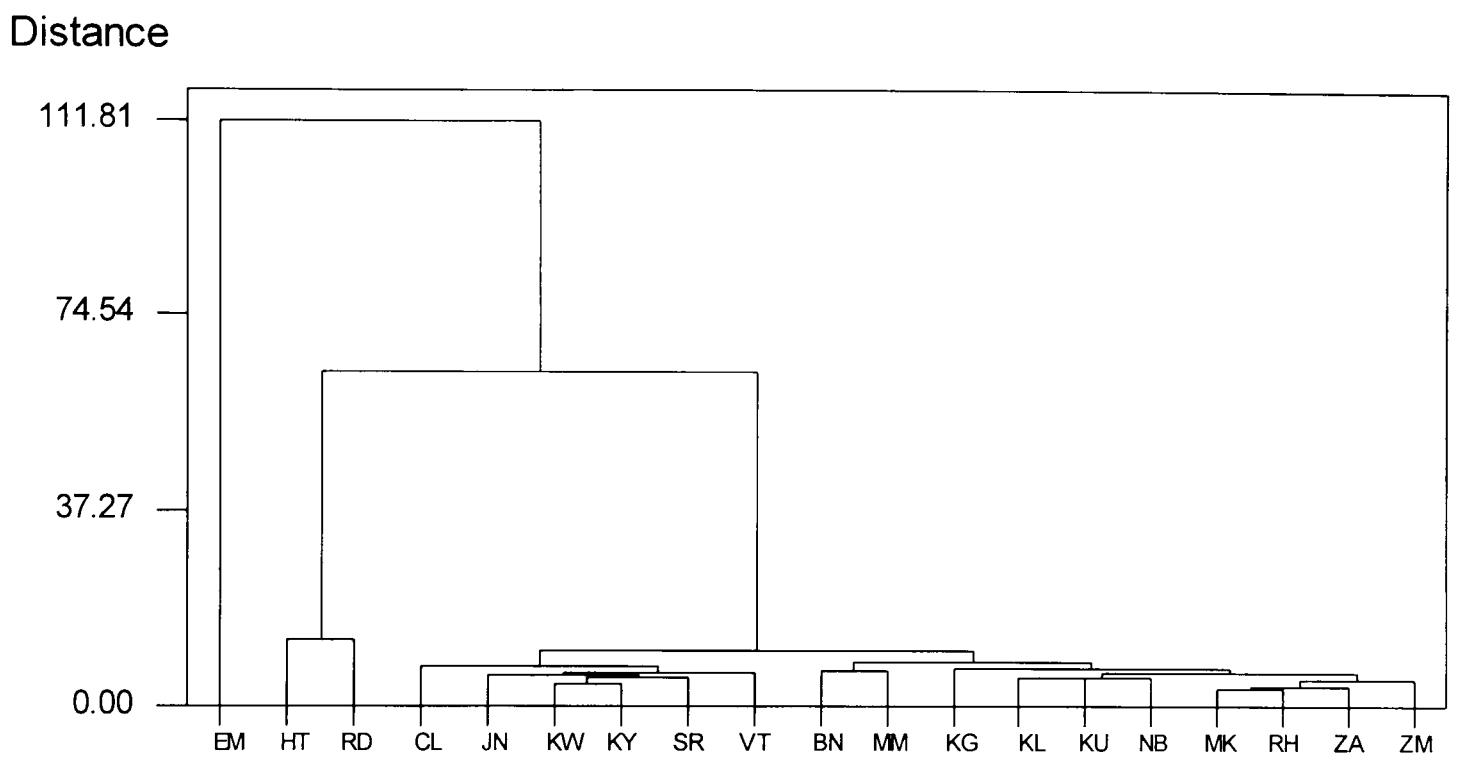


Fig 8.7 Dendrogram Showing Male Association Patterns During *FOOD RICH* Periods

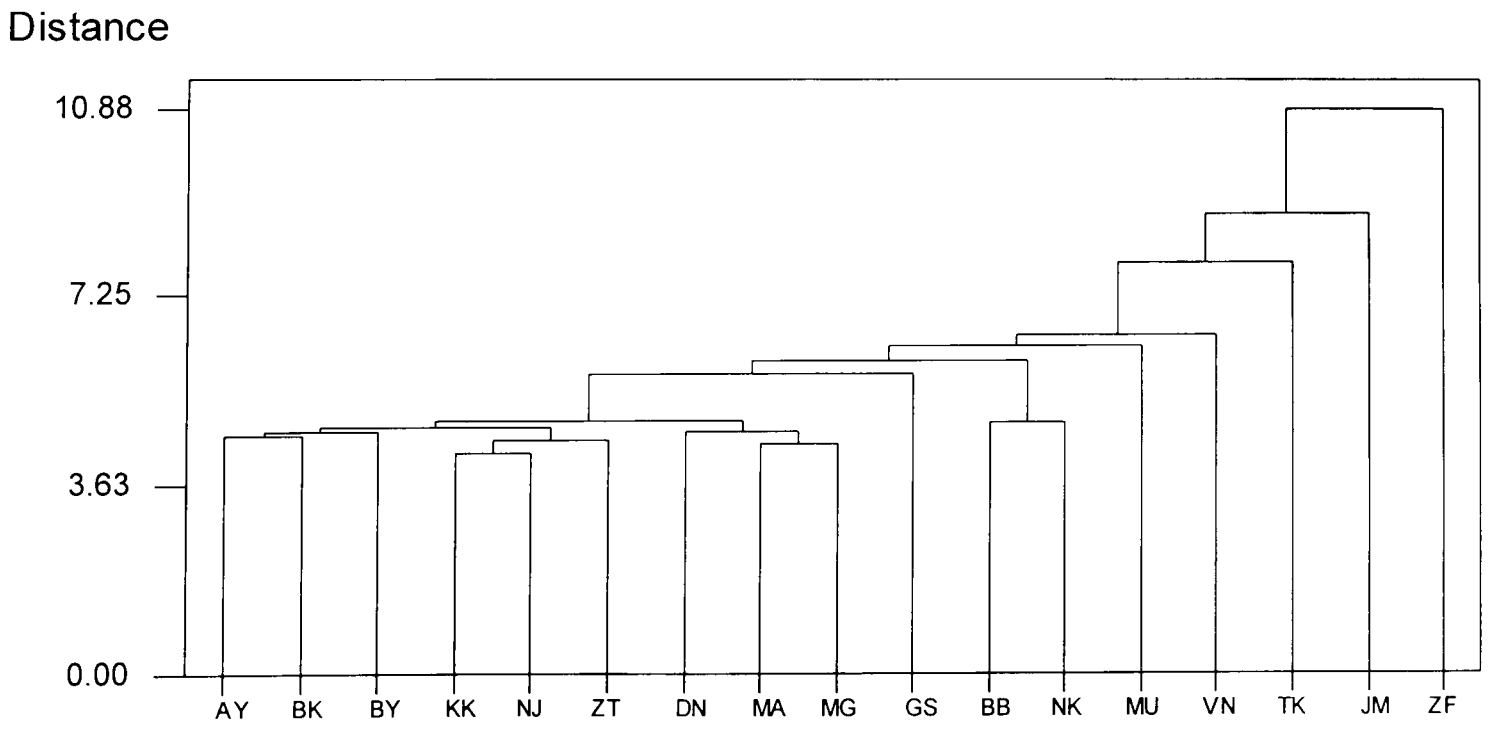


Table 8.6 Mean Dyadic Association Indices For Each Sex Category During The *Food rich* Period.

Dyad	N	Mean	Median	St dev	SE mean	Min	Max
male-male	120	0.162	0.162	0.045	0.004	0.061	0.237
male-female	288	0.123	0.132	0.058	0.003	0.000	0.268
female-female	153	0.120	0.128	0.066	0.005	0.000	0.313

Table 8.7 Mean Dyadic Association Indices For Each Sex Category During The *Food poor* Period.

Dyad	N	Mean	Median	St dev	SE mean	Min	Max
male-male	120	0.099	0.090	0.049	0.004	0.010	0.250
male-female	288	0.063	0.050	0.049	0.003	0.000	0.220
female-female	153	0.058	0.040	0.064	0.005	0.000	0.230

In both the *food rich* and the *food poor* periods the median strength of male-male association was significantly greater than the median strength of female-female, (*food rich* W=20131.5, $p<0.001$; *food poor* W= 20438.0, $p<0.0001$), or male-female dyads (*food rich* W=31164.0, $p<0.0001$; *food poor* W=31049.5, $p<0.0001$). In addition, for all sex categories the median DAI was significantly greater (i.e. individuals showed closer association) during the *food rich* period compared to the *food poor* period, (male-male W=19053, $p<0.0001$; male-female W=105374, $p<0.0001$; female-female W=29570.5, $p<0.0001$). Furthermore, the median association between females during the *food rich* period was significantly greater than that between males during the *food poor* period (W=14583.5, $p<0.01$). Thus, to summarise generally, during periods of increased food availability the association indices of all dyads increases. This is in agreement with the findings in Chapter 5 that group size correlates with measures of food availability.

In order to investigate in more detail the effect of changes in food availability on the choice of associates, a Kruskal-Wallis test was performed to test for significant differences in the median association indices between different life history classes. The life history classes used were adult and adolescent males, adult and adolescent females and cycling and non-cycling females (see Tables 8.8 & 8.9).

During the *food rich* periods there were no significant differences between the median association indices of adult females and any of the life history classes. (H=6.73, ns). However, during *food poor* periods there was a significant difference (H=20.58, $p<0.0001$). With the Kruskal-Wallis test it is not possible to say which

Fig 8. 8 Dendrogram Showing The Association Patterns Of The Sonso Community During The *FOOD POOR* Period

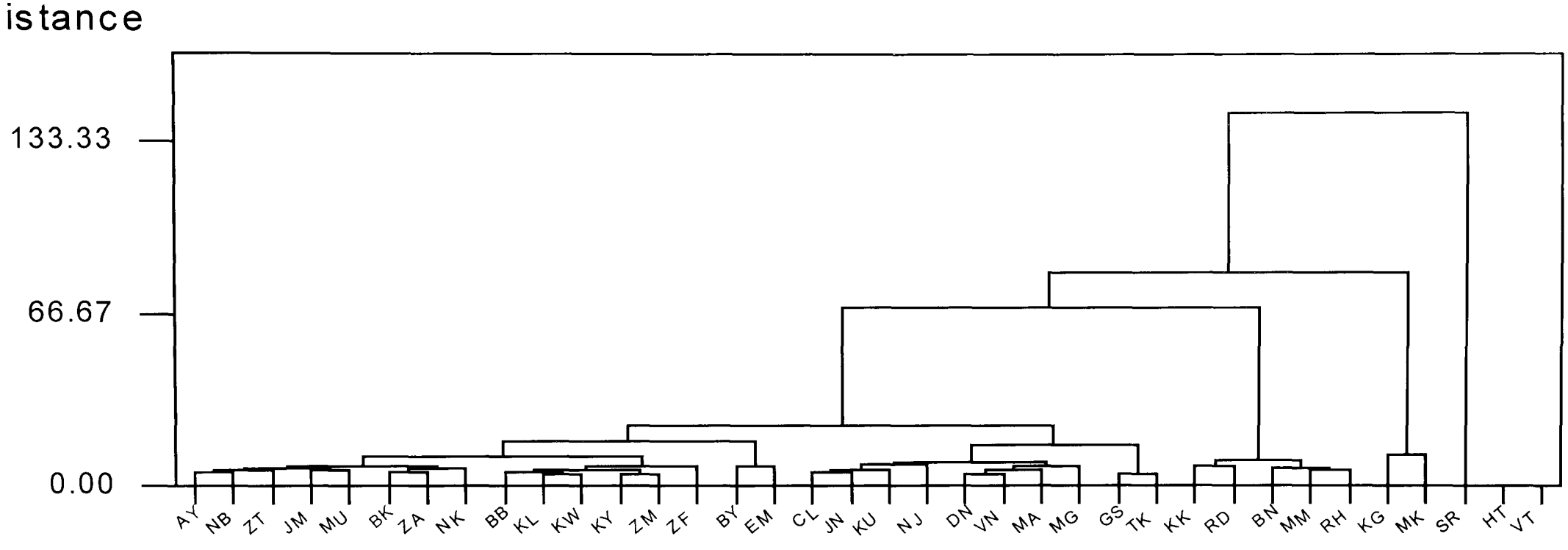


Fig 8.9 Dendrogram Showing Female Association Patterns During *FOOD POOR* Periods

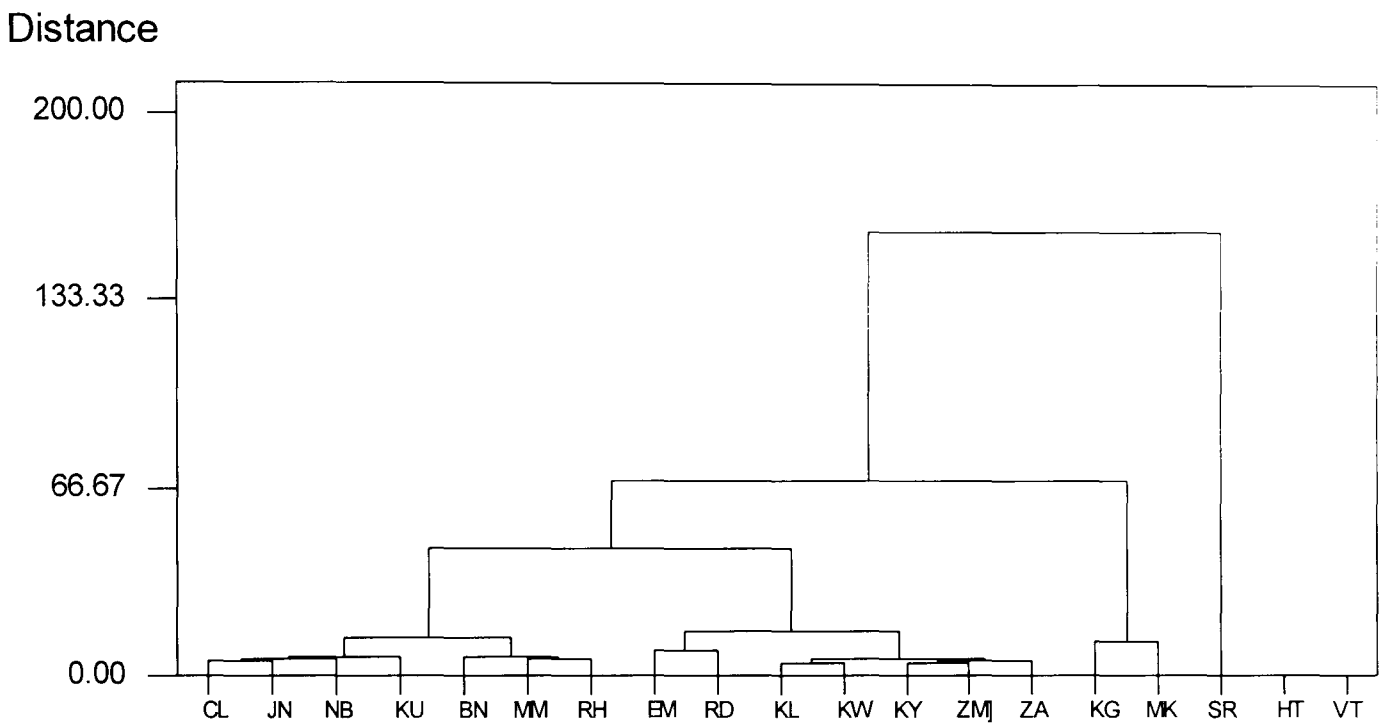
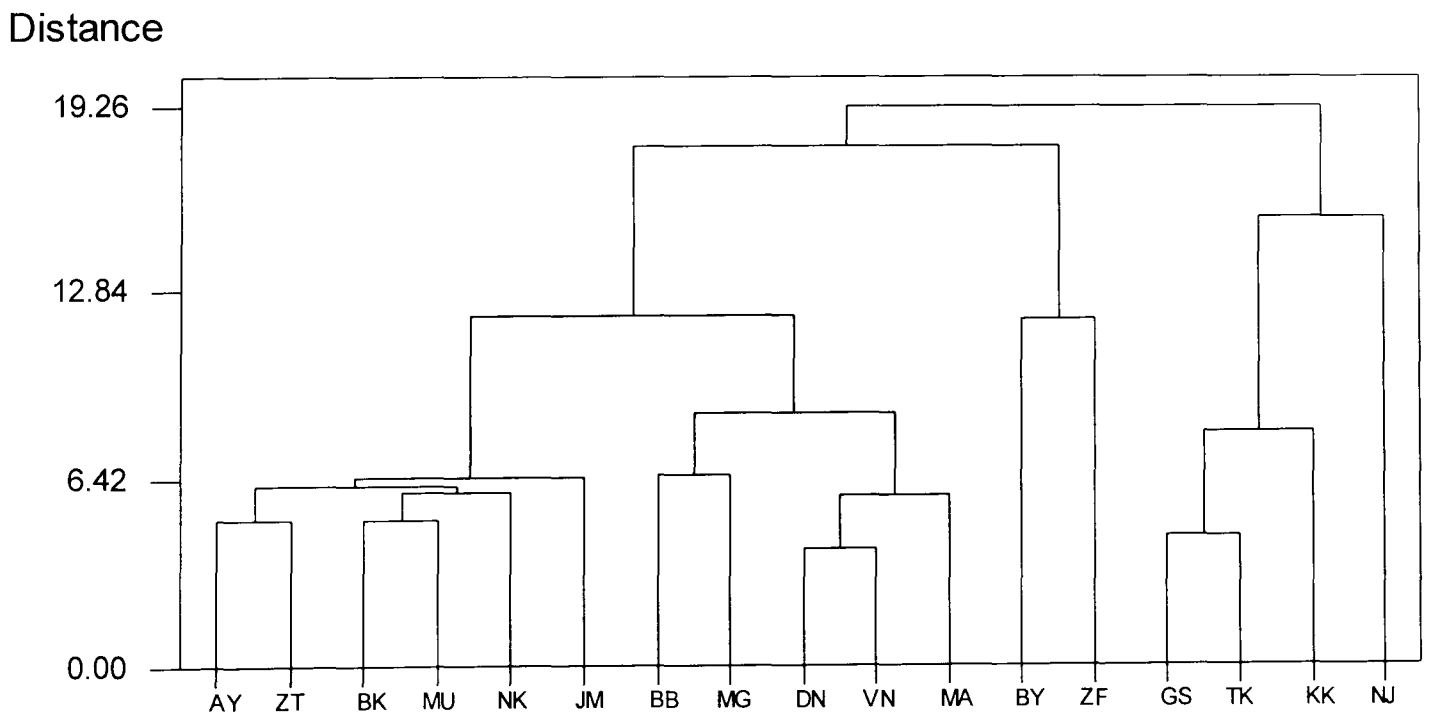


Fig 8.10 Dendrogram Showing Male Association Patterns During The *FOOD POOR* Period.



variable(s) is significantly different, however inferences about the maximum and minimum value may be made and interpreted in a logical manner (Fowler & Cohen, 1998). During *food poor* periods, adult females had the lowest association with adolescent females and adult males, and the closest association with adolescent males and adult females. On the other hand, adolescent females showed no significant differences in their association patterns during *food poor* periods (H=6.65, ns) and significant differences during *food rich* periods (H=13.34, $p<0.01$), when their closest associates were adolescent males and they had least association with adult females. The adult males preferred to associate with each other in both food periods (*food rich* H=54.05, $p<0.0001$; *food poor* H=54.47, $p<0.0001$). Adolescent males did not show significant association with any life history class in either period (*food rich* H=6.33, ns; *food poor* H=7.55, ns). Non-cycling females followed a similar pattern to that of the adult females; no significant differences in association patterns during the *food rich* period (H=2.14, ns) and a significant difference in the *food poor* period (H=12.31, $p<0.01$), with maximum association indices with adolescent males and minimum with adult males. Cycling females showed a similar pattern to that of the adolescent females; significant differences during the *food rich* period (H=13.78, $p<0.01$), with maximum association indices with adolescent males and minimum association indices with non-cycling females. During *food poor* periods, cycling females showed no significant differences in patterns of association (H=5.07, ns). When the association patterns of the different life history classes were analysed for the whole study period, the patterns were generally the same as those during the *food rich* period, the exception being adolescent males which showed significant differences in their association patterns (H=32.43, $p<0.0001$), showing overall maximum association with other adolescent males and minimum association with adult females.

Even though generally all association indices categories were significantly less during the *food poor* period, it was possible that some dyads may have had a different response to the presumed increased feeding competition during the *food poor* period. To investigate this, association indices of dyads which were identified

Table 8.8 Mean Dyadic Association Indices Between Different Life History Categories During The *Food Rich* Period, (Italics = S.E., ( ) = sample size).

	Adult Female	**Adolescent Female**	**Adult Male**	**Adolescent Male**	**Cycling Female**	**Non-cycling Female**
Adult Female	0.132 *0.007* (66)					
Adolescent Female	0.109 *0.008* (72)	0.111 *0.020* (15)				
Adult Male	0.115 *0.005* (144)	0.135 *0.008* (72)	0.174 *0.005* (66)			
Adolescent Male	0.120 *0.008* (48)	0.136 *0.012* (24)	0.148 *0.007* (48)	0.143 *0.021* (6)		
Cycling Female	-	-	0.143 *0.009* (96)	0.144 *0.005* (32)	0.129 *0.008* (28)	
Non-cycling Female	-	-	0.104 *0.005* (120)	0.111 *0.010* (40)	0.118 *0.008* (80)	0.116 *0.011* (45)

Table 8.9 Mean Dyadic Association Indices Between Different Life History Categories During The *Food Poor* Period, (Italics = S.E., ( ) = sample size).

	Adult Female	**Adolescent Female**	**Adult Male**	**Adolescent Male**	**Cycling Female**	**Non-cycling Female**
Adult Female	0.076 *0.008* (66)					
Adolescent Female	0.043 *0.007* (72)	0.028 *0.014* (15)				
Adult Male	0.049 *0.005* (144)	0.053 *0.007* (72)	0.100 *0.100* (66)			
Adolescent Male	0.082 *0.009* (48)	0.063 *0.011* (24)	0.095 *0.09* (48)	0.120 *0.011* (6)		
Cycling Female	-	-	0.588 *0.006* (96)	0.071 *0.009* (32)	0.052 *0.011* (28)	
Non-cycling Female	-	-	0.053 *0.005* (120)	0.095 *0.012* (40)	0.055 *0.007* (80)	0.069 *0.011* (45)

as being important throughout the course of the study were compared during *food rich* and *food poor* periods. These included 6 male-male dyads (DN VN, NJ ZT, AY MA, AY BK, AY DN, BK BY) and 5 female-female dyads (JN CL, KU NB, KY ZM, KL KU, KW KY). For all male dyads, except DN VN, there was a decrease in the dyadic association indices during the *food poor* period. It is possible that the increase in the DAI between DN and VN during the *food poor* period was an indirect result of VN being absent for two weeks during the *food rich* period. This absence was unusual and not correlated with an absence of any of the other community members. He was last seen on a day when the chimpanzees visited the edge of the community range to the south east. He returned with another adult male, Muga (MG), one month later, while the chimpanzees were feeding in the core of the community home range. Of the female-female dyads, two (JN CL and KY ZM) showed an increase in association during the *food poor* period, whereas the other three dyads showed a decrease in the strength of their association. Both of these dyads included cycling, adolescent females suggesting differential benefits of female-female association in the *food poor* period for females of different life history classes.

8.6 Discussion

The association patterns among the Sonso community of chimpanzees resembled those reported from other East African study sites (Goodall, 1986; Wrangham et al. 1992; Nishida, 1979). The closest associations were between males, followed by similar association patterns between the sexes and between females. Further investigation into the dyadic relationships between females showed a greater degree of variation between female-female relationships than between those of males. Particular female-female dyads were seen together with similar frequencies to the male dyads, whereas other females were loosely associated with both the males and females of the community. This suggests that, at least for some dyads or individuals, the cost of grouping is less than in other east African communities. At Kibale Forest, all female dyads were less closely associated than male dyads (Wrangham, 1992).

Close associations between females were observed at Gombe, but only between mother and daughter (Goodall, 1986).

There were no obvious persistent sub-groups of females within the community, except perhaps the association of Janie (JN) and Clea (CL) and that of Nambi (NB) and Kutu (KU). Nishida (1989) showed that, even six years after the integration of two communities, there were still differences in the association patterns between the initial resident females and the more recently immigrated females. For the Sonso community, it was impossible to know to what extent historical events were reflected in the present association patterns. Ongoing DNA analyses may help to distinguish kin-based patterns of association.

The analysis of female dominance interactions confirmed that female-female competition exists and provides evidence of a dominance hierarchy, although it was not possible to assess the linearity of this hierarchy. As observed in Arnhem (de Waal, 1982), the majority of dominance interactions were pant grunts which serve to reconfirm existing dominance relations rather than challenges to the rank order. There is some evidence that rank position is correlated with age. All adult females were dominant to all adolescent females. However, within the adult female class, it was not possible to clearly associate age with rank. This was due to difficulties of assigning correct ages and also the lack of dominance interactions between certain dyads. It was the observer's opinion that Kutu (KU), due to her overly protective behaviour of her infant Kato (KT), was a first time mother. Kalema (KL) and Kwera (KW) were also thought to be young mothers, judged by appearance and the lack of obvious juvenile offspring. Kwera was seen to associate with Bwoba (BB), a adolescent male frequently, however he is not thought to be her son, but the son of Zana (ZN). Zana is severely handicapped, which probably affects her association levels. It is possible that Kwera has taken on the role of adoptive mother. Whilst Bwoba was a juvenile he also used to associate with Kwera (G. Muhumuza pers com.).

In addition to the general association patterns of the females of the Sonso community, certain females had particularly interesting relationships and they are discussed below as case studies.

Nambi (NB)

The data on female hierarchies show clearly that Nambi is the alpha female. In addition, the analysis of association data showed Nambi to be the only adult female to have another female as a close associate, Kutu (KU). Boesch & Boesch-Achermann (2000) also noted that the dominant females were the females with close alliance partners. It was not possible to accurately assign a rank position to Kutu in the dominance hierarchy, but she appears not to be the Beta female. Nambi and Kutu were close associates in the analyses of overall association patterns and during the *food rich* period. However, in the *food poor* period, although still close associates, Nambi showed closer association to her son, Andy, and adolescent females Janie (JN) and Clea (CL). Nambi was also observed to have the closest association with the males of all adult females. This was true even when the high association value of Nambi and her adolescent son Andy (AY) was removed from the analyses. In addition, Nambi was the only adult female to include the alpha male, Duane (DN) in her top five close associates. This indicates that there may be social benefits as well as possible foraging benefits associated with high female rank. Chapter 7 shows that she had the largest home range of all the adult, non-cycling females. Nambi also has the greatest number of offspring; MU, AY, MS, NR. and her daughter Nora was observed to play with the adult males, whereas no such interaction was observed with the infants of the other females.

Clea (CL)

The dominance data show that the majority of all dominance interactions involved adolescent females, with the most recent immigrant female, Clea, both receiving the most aggression and reconfirming most often her submissive relationships by pant grunting. When Clea was first seen in the community during the early months of 1997, she associated with males, mainly in sexual parties (pers. obs.). At this time Clea was not observed to have a full sexual swelling or to be mated by the community males. She appeared to be a young female. After three or four months she was seen regularly with the community, however she was not observed to have a full sexual swelling until late in 1998. Clea received aggression from both resident adult

and adolescent females and other immigrant females. Slowly, Clea integrated into the community and was observed to associate with females when males were not present. On one occasion Clea was observed to play with Nora, (the infant of Nambi) whilst Nambi was feeding some distance away in the same tree. No other female was observed to play with the infant of another female. The immigrant females Clea and Janie (JN) had a close association index. Perhaps adolescent females form alliances or coalitions with each other in order to ease the process of integration into a new community. It is certain that Janie immigrated into the community before Clea, but they possibly came from the same natal community, which may facilitate alliance formation. If females were forming alliances during the process of integration in to a new community, this would explain why female alliance partners at Tai Forest were of similar age and rank (Boesch-Boesch-Achermann, 2000).

Kewaya (KY)

In contrast to the immigrant females, Keweya remained in her natal community to raise her first offspring. Kewaya gave birth in December 1998. All dendrograms show a close association between mother, Zimba (ZM) and daughter, Kewaya. At Gombe, the closest of all associations were between mother and offspring (Goodall, 1986). It is possible that this close alliance between mother and daughter was important in the decision for Kewaya to stay in the community. Due to lack of serious aggressive interactions between resident females and resident adolescent females, Pusey (1980) concluded that female transfer was voluntary in spite of aggression received from females in the new community. She suggests that females are attracted to unfamiliar males, and describes oestrous females as continuing to move towards the calls of another community when the adult males of the natal community turned back (Pusey, 1979). Contrary to observations by Pusey (1980), Kewaya *did* experience agonistic interactions with adult females in the natal community; in addition she was observed to pant-grunt less frequently to adult females in comparison to immigrant, adolescent females. However, these dominance interactions were not corrected for the number of observation hours on each individual. Kewaya was also the only female observed to take part in what could be

considered a sexual consortship (Tutin, 1979). She was observed to associate only with Kikunku (KK) for two days. They copulated frequently, and, interestingly, they both spent a night in nests on the ground.

The social relationships of some of the females with the rest of the community still remain somewhat ambiguous. Emma (EM), Ruda (RD), Banura (BN), Mama (MM), Harriet (HT) and Vita (VT) all had a distinctly lower association indices with the rest of the community. In the case of **Ruda** and **Harriet** this may be explained by the more shy females taking longer to habituate. Both females were very shy, and could not be followed on the ground. They remained high in trees when alone or with other individuals. These females were seen in the centre of the community range. Interestingly, Harriet was always seen in the same area (to the west of the sawmill area), both when alone or associating with other individuals. **Banura** was also a shy female and the ranging data showed her to have a peripheral range. In addition, Banura was old and handicapped with a congenital swelling of her right foot, which probably affected her association patterns. Her adolescent son was similarly peripheral to the other male association patterns. **Mama's** association with the community was also ambiguous. She was usually observed only when in oestrus, when she was popular with the males. She was rarely observed in the core area of the community range. Her adolescent daughter began to travel independently with the community towards the end of 1998. **Emma** was a juvenile female believed to be an orphan. When initially seen with the Sonso community in late 1997, she associated with Magosi (MG), the ex-alpha male, as the rest of the group moved away from the feeding tree. Then she was observed to be sick, suffering from diarrhoea. It is unknown if she is the orphan of a then unknown peripheral female or if she had immigrated from another community. She was seen intermittently until 1998 when she was regularly seen associating with members of this community. **Vita** was a adolescent female that sometimes associated with the Sonso community. She had no obvious relatives in this community and was never seen to copulate with the males. She was not observed to exhibit a full sexual swelling and would appear in the community with or without any signs of sexual swelling. She was also not involved in any aggressive interactions with the females. She was not observed during the

period of food scarcity and therefore perhaps belongs to a neighbouring community and visits the Sonso community only during times of high food availability. It will be interesting to see if she ever fully integrates into the Sonso community. Goodall (1986) also reported temporary visits of immigrant females.

Other 'stranger' females were observed in the community from time to time. These included females with and without infants. Due to the difficulties in identifying females which are rarely seen it is impossible to know if the same females were observed more than once. Usually, the females were showing full sexual swellings and were the target of much interest from the adult males. On one occasion, an unidentified adult female with a female juvenile were observed feeding peacefully for a morning with only community females, and on another occasion Kewaya and Zimba were observed to form an alliance to chase an unknown female over a distance of at least 100m in the absence of males. The only other coalition between females was observed between Ruhara (RH) and Sara (SR) against Kalema (KL). They co-operated to prevent Kalema entering a feeding tree, (after a while Kalema then entered and fed in the tree). It is possible that Ruhara and Sara could be mother and daughter. Sara was an interesting female, she had no known infant and was therefore classified as a adolescent female, however, her appearance suggested she was older. She had a small bald patch and white hairs around the chin. In addition, she was never a popular copulation partner when in oestrus.

The analysis of association patterns suggests that the alpha female maintains high association indices with the adult males. Thus, females may be competing for social benefits in addition to food resources. An adult female may benefit from association with males through protection from infanticide, and, in addition, she is in a position to support her male adolescent offspring in conflict encounters with other males. Boesch & Boesch-Achermann (1997, 2000) found that dominant females invested approximately two years more in the raising of sons than in daughters. Mothers at Tai were observed to actively support sons in social life. The increased investment in sons may be considered an evolutionary strategy to increase the reproductive success of the female. A male can potentially father far more offspring during his life time than a female can produce. Therefore, if a female can improve the

ability of her son to gain mates, she should invest in sons. However, if she cannot influence her son's success, she should play it safe and invest in daughters, who will produce a limited but more certain number of offspring. This trend has not been observed at either Gombe or Mahale.

Analyses of the strength of associations in *food rich* and *food poor* periods showed that all sex categories of dyads, i.e. male-male, male-female and female-female, showed significantly greater affiliation during the period of higher food availability. Two of the adult females, Harriet (HT) and Vita (VT) were not observed at all during the *food poor* period. It was interesting to note that during the time of high food availability, the mean DAI between females was significantly greater than the mean DAI between males during the *food poor* period. This illustrates a significant overlap in the range of association patterns of the two sexes. The results of Chapter 5 showed that group size was significantly correlated with the availability of food, and this chapter documents how the change in food supply affected the choice of associate. These results suggest that the choice of associate during the times of different food availability was different for the different age/sex categories. In both periods of food scarcity and abundance, adult males were observed to preferentially associate with each other. This highlights the constant benefits of male association suggested in chapter 5. In contrast, adult females showed no significant preference for a particular class of associate during the *food rich* period, but during the *food poor* period preferentially associated with adolescent females and adult females. According to Boesch & Boesch-Achermann (2000), female alliances are a response to increased feeding competition between females. This idea was tested by looking at the change in association patterns of certain dyads in *food rich* and *food poor* periods. Out of five female-female dyads that were stable throughout the study period, only two showed an increase in association strength during the period of food scarcity. Thus, although adult females as a category associated preferentially with adolescent males and other adult females during the food poor period, generally they did not increase their association in particular female-female dyads. The two female-female dyads which showed an increase in association strength in the *food poor* period both included adolescent females; one dyad were mother and daughter. From

data on dominance interactions, it appears that within the category of females, adolescent females experience the most aggression. Feeding competition will be most significant during periods of food scarcity. In addition, they do not have the energetic cost of carrying and feeding an infant. Therefore they may be able to tolerate feeding competition from a companion.

These results suggest that the period of extreme food shortage had a significant effect on the choice of associates. All dyads displayed weaker association during this period and adults tended to associate with same sex individuals or their offspring. In contrast, to the consistent choice of male chimpanzees to associate with each other, female associate choice varied food availability.

8.7 Conclusions

- Analysis of general association patterns shows male-male dyads to be bonded significantly closer than either male-female or female-female dyads. There was no significant difference between the average association indices of male-female dyads and female-female dyads.
- Closer examination of individual female-female dyads showed there to be great variation in the extent of bonding between individual dyads. Some dyads were as closely bonded as male dyads.
- Analysis of association patterns during times of high and low food availability showed association indices of all categories decrease in times of low food availability.
- Female dominance relations did exist in the Sonso community, with the majority of dominance interactions involving adolescent females.
- Data from this study and others suggest that the most important period in the life history of a female for resource competition is when integrating into a new community. During the process of immigration, as predicted by sexual selection, females are competing with other females rather than with males. However, once established in a new community, data from this study and others suggest that there are fewer dominance interactions and that dominance hierarchies remain stable.

- It is suggested that females may be competing for both access to food resources and social opportunities.

Chapter 9

The Behavioural Ecology of the Sonso Chimpanzee Community: A Concluding Discussion.

The extent of behavioural diversity between chimpanzee communities is increasingly apparent as more data are collected from different habituated communities. The only feature of chimpanzee social organisation which appears to be common across all populations studied to date is the fluid fission- fusion society within multi-male communities. Cultural differences in tool use behaviour, social traditions and hunting behaviour (Whiten et al. 1999; Boesch & Boesch -Achermann, 2000). Most intriguingly, as discussed in this thesis, the nature of female social relationships, in particular the strength of female-female association differs between communities (Goodall, 1986; Wrangham et al., 1992; Baker & Smuts, 1994; Boesch-Boesch-Achermann, 2000). The variation in female relationships could reflect different strategies to efficiently exploit food resources under different ecological conditions (Wrangham, 1980; van Schaik, 1989; Sterck, 1997). Studies of forest living chimpanzees have shown that differences between the female bonded *P. paniscus* (White, 1988; Kano, 1992) and the male-bonded *P. troglodytes* (Goodall, 1986) social organisation, once thought to be uniquely different social organisations, may simply reflect a continuum of different social and/or ecological conditions (Stanford, 1998; Boesch & Boesch-Achermann, 2000). Boesch & Boesch-Achermann (2000) propose that the forest living chimpanzees at Tai experience stronger intra-group competition than those living in the woodland/gallery forest habitats. Under such circumstances it may be more advantageous for females to form strong bonds. They suggest that both bonobo and chimpanzee females maintain social cohesion by extending the duration of their sexual swellings and increasing their association and alliances with females.

This study addressed how the temporal variation in food supply was reflected in the behavioural patterns of the Sonso community chimpanzees.

Budongo Forest Ecology

Budongo forest was found to exhibit four seasons as defined by climatic variables. These translated into periods of alternating high and low food availability for the chimpanzee population. The patterns of food availability were closely synchronised for all plant parts eaten by chimpanzees and the availability of chimpanzee foods was found to be closely related to the production rhythms of the forest community as a whole. These production patterns were linked to the climatic variables of irradiance and rainfall. The dry seasons were associated with lower levels of food availability, with the second and shorter dry season experiencing the most severe food shortage. This was due to a combination of both low rainfall and low irradiance levels. During the longer dry season between the months of December and February there was a peak in the fruit abundance of *Ficus spp.* coinciding with a reduction in non-fig fruits. *Ficus spp.* may therefore provide a potential keystone food at such times. Throughout the study period, *Ficus sur* and *Broussonettia payrifera* were identified as important keystone foods. *F.sur* had an asynchronous fruiting pattern and was therefore available throughout most of the year; whereas *B. payrifera* had two distinct fruiting periods which coincided with the two dry seasons. Phenology patterns emphasised the importance of a variety of keystone species to maintain chimpanzee diets during periods of low food availability.

Chimpanzee Behavioural Responses

Both the feeding and association patterns of the chimpanzees changed in response to the availability of food. Party size was positively correlated with measures of food availability, suggesting a constant benefit to grouping (van Schaik, 1999). A frequent predictor of party size was the combined measure of abundance of fruit, flowers, buds and leaves, highlighting the importance of leaves, in addition to fruit, in the diet of the chimpanzees at Budongo. Different types of parties responded differently to changes in food supply. In particular, the size of sexual and all-male parties was

positively correlated to levels of food availability. In addition, both the number of males and females in sexual parties and the number of females in mixed parties increased when food was abundant. However, the size of all-female parties was not correlated with any measure of food availability. This suggests different association strategies of the sexes. During times of high food availability males formed larger all-male parties and joined sexual parties, whereas females maximised their association in mixed groups. Analysis of dyadic association patterns showed that during the two extreme periods of food shortage and food abundance, adult males consistently showed closer association patterns with each other than any other category. In contrast, adult females, although preferentially associating with adolescent males and adult females during the period of food shortage, showed no significant preference for a particular age/ sex class of associate during the period of high food availability.

The sexual behaviour of the females were also found to be correlated with measures of food availability. The number of females in the community exhibiting full sexual swellings increased during times of high food availability. The sizes of all-male and sexual parties were significantly correlated with the number of oestrous females in the community. However, the number of males or females in any party type was not correlated with the availability of oestrous females. General Linear Models were used to show that measures of food availability were the best predictor of both party size and the number of females in oestrus. This suggests that food availability was an independent variable determining both party size and the number of oestrous females in the community. Cycling females were found to spend significantly more time moving than non-cycling females, and there was a trend for this to be correlated with a decrease in feeding time. Perhaps during times of high food availability females were better able to tolerate a reduction in feeding time.

Dietary and activity patterns showed that the chimpanzees had a flexible response to changes in food availability. The general tendency was for the chimpanzees to decrease the proportion of time spent moving and feed on lower quality food items during periods of low food availability. However, during the period of the most extreme food scarcity, the chimpanzees were observed to increase

the time spent moving and to travel beyond the normal community range to find food. There was evidence that both young leaves and THV are keystone food resources during times of fruit scarcity. In addition, the young leaves of *C. mildbraedii* were a highly preferred food item at certain times of the year.

The observation that chimpanzees maintained a frugivorous diet during periods of food scarcity is consistent with the predictions of the ecological model of social organisation (Wrangham, 1980; van Schaik, 1989; Sterck, 1997). It is proposed that the flexible nature of fission-fusion groups is the result of the combination of intense scramble feeding competition particularly during periods of food scarcity, large body size and the, perhaps physiological, requirement of the chimpanzees to maintain a frugivorous diet (Wrangham, 1979a, 1980). Females are thought to be more sensitive to the effects of feeding competition and thus female chimpanzees are predicted to be less sociable than males during times of food scarcity. Results from this study suggest that in general, decreases in food availability are correlated with a decrease in time spent moving and a lower quality diet: a strategy to reduce energy expenditure. However, it is evident that during extended periods of extreme food shortages this is no longer a viable strategy and the chimpanzees will increase the time spent moving in order to find food resources. This period was also associated with generally smaller party sizes. Analyses of the dyadic association patterns showed that in all age/sex categories the median dyadic association strength was significantly less during the period of low food availability. It is hypothesised that as a result of feeding competition during the period of extreme food shortage, the development of female alliances is impossible. This is in contrast to preliminary data on bonobos which suggested that despite fluctuations in food availability, females are able to maintain social cohesion (White, 1998). The Tai Forest experiences no distinct dry season (Boesch & Boesch-Achermann, 2000) and thus perhaps no such period of extreme food shortages in comparison to the more seasonal forest and woodland habitats of east Africa.

The Nature of Female Social Relationships

The analyses of the individual ranging patterns of males and females provided evidence of a bi-sexual community. All the core areas of the females, including the peripheral females, were found well within those of the male community range. This suggests that there may be some risk associated with ranging at the edge of the community range. This risk may be a reason why females choose to associate with males of a specific community. Ecological theory predicts that females should distribute themselves according to the food distribution and males in turn distribute themselves according to the distribution of females and the acquisition of mating opportunities. When the females are highly dispersed as in the chimpanzees it is profitable for the males to form groups (Dunbar, 1988). In addition, females may respond to the distribution patterns of the males by avoiding the boundary areas of the community range and thus the risk of infanticide or harassment from neighbouring groups of males. Males have been observed to attack stranger females and kill their infants, which results in male coercion of the female into the community range area of the males (Goodall, 1986). Therefore, females may choose to form groups, even loose ones, in order to prevent this harassment from stranger males.

In agreement with other studies of East African chimpanzees (Wrangham, 1979; Wrangham & Smuts, 1980; Hasegawa, 1990), and in contrast to the chimpanzees at Tai (Boesch, 1991), the size of individual female core areas was significantly smaller than those of males. The life history category which most influenced the size of female core areas was whether or not a female was cycling during the study: cycling females were found to have larger core areas than non-cycling females. Based on their ranging patterns within the community range, females could be identified as either peripheral or central. That said the individual core areas of females overlapped extensively, many of the central female core areas completely overlapped each other. The size of male and female core areas was similar to those found at Gombe (Wrangham & Smuts, 1980). Due to the higher density of chimpanzees in the Budongo Forest and the overlapping nature of the

individual female ranges it follows that females have a greater opportunity for association in Budongo than in Gombe.

Dyadic association patterns also showed that, in agreement with all other communities studied, the association strength between males was the greatest with no significant difference between the association patterns of male-female or female-female dyads. Further analysis of individual dyadic relationships showed there to be great variability in the extent of association between females. Some females showed considerably lower association patterns to other community females and males, but between particular female dyads association strengths were similar to those between males. This is in contrast the association patterns of females at Kibale Forest and elsewhere in East Africa (Nishida, 1979; Goodall, 1986; Wrangham et al., 1992). However, overall the closest dyadic relationships were between males.

Dominance relationships between females exist. The data do not preclude the possibility of a linear hierarchy, however, many females were not observed to interact. There is the clear emergence of an alpha female which suggests the importance of dominance in the shaping of female relationships. There were many dominance interactions, both formal and agonistic, between the adult and adolescent females. This provides evidence of contest feeding competition. Sterck et al. (1997) stated that where there is strong contest competition there will be evidence of formalised dominance, using signals of dominance i.e. pant grunts. In addition, females were observed to resist the immigration of other females into the community. The period of transfer between communities is the most important period during a female's life history in terms of resource competition. Strong intra-group contest competition also predicts female alliances. These were not observed in this community, however, occasional opportunistic female coalitions were observed, these were between possible mother-daughter dyads as predicted. If females obtain constant benefits from grouping, a positive correlation between all-female group size and food availability is expected (van Schaik, 1999). This was not found. Instead the number of females in mixed groups increased with food availability. I suggest females may join groups in order to gain social benefits. There was some evidence that for adult females high rank was associated with an increase in core area size.

Association patterns also suggest that the alpha female had closer association with the alpha male and other adult males. I suggest that contest competition between females may be important for determining party composition and this is reflected in the differential reproductive success observed at Gombe (Pusey et al., 1997)

In summary, the nature of female relationships and the strategies of the chimpanzees to periods of low food availability support the argument that the fission-fusion social system is a response to high levels of feeding competition. As a result of the fission-fusion social system, the feeding competition experienced by females is probably a mix of scramble competition in the locating of food resources (Wrangham, 2000) and contest competition for membership of feeding parties at food patches and the resultant social opportunities. Although forest living, and despite the fact that the ranging data suggests greater opportunities for female association and some female dyads associated as closely as males, the social organisation of the Budongo chimpanzees was found to closely resemble that of the Gombe and Mahale communities. This is in agreement with studies of the Kibale Forest chimpanzees (Wrangham et al., 1992), and in contrast to the Tai Forest community (Boesch & Boesch-Achermann, 2000). It can be expected that the social organisation of a species will reflect the selection pressures imposed by critical periods of food shortage. In conclusion, I suggest that the high degree of seasonality in food production and in particular the periods of extreme food scarcity may preclude social cohesion and the formation of female alliances in this community of chimpanzees.

APPENDIX A

Checksheet Used To Collect 15min Scan Data

Chimp name		Observer		Method of Location				Date	
Time									
Block									
Activity									
Food Spp./Item									
DBH									
Phen. Score									
Group dispersal									
Banura	Bn								
Harriet	Ht								
Mama	Mm								
Nambi	Nb								
Ruda	Rd								
Ruhara	Rh								
Zimba	Zm								
Kigere	Kg								
Zana	Za								
Kwera	Kw								
Kalema	Kl								
Kutu	Ku								
Kewaya	Ky								
Sara	Sr								
Janie	Jn								
Mukwan	Mk								
Clea	Cl								
Muhara	Mh								
Vita	Vt								
Gonza	Gz								
Shida	Sh								
Grinta	Gt								
Magosi	Mg								
Tinka	Tk								
Duane	Dn								
Vernon	Vn								
Maani	Ma								
Bwoya	By								
Jambo	Jm								
Nkojo	Nj								
Black	Bk								
Chris	Ch								
Muga	Mu								
Kikunku	Kk								
Zesta	Zt								
Andy	Ay								
Zefa	Zf								
Nick	Nk								
Bwoba	Bb								
Gashom	Gs								
Kadogo	Kd								
Musa	Ms								
Bob	Bo								
Kato	Kt								

APPENDIX B.1

Index Of Food Availability For Chimpanzee Food Species For Each Phenological State Using Only The DBH Value Of The Fruiting Tree As A Measure Of Abundance. (BD = buds, YL = young leaves, ML = mature leaves, FL = flowers, UR = unripe fruit, HR = half ripe fruit, RF = ripe fruit).

Period	BD	YL	ML	FL	UR	HR	RF
SEP 97 (1)	0.59	21.13	99.20	9.45	15.23	33.77	78.18
SEP 97 (2)	45.36	45.65	99.11	11.26	10.54	25.03	100.00
OCT 97 (1)	9.53	77.83	99.33	55.09	13.11	7.04	56.58
OCT 97 (2)	6.90	49.70	99.59	0.76	13.45	3.70	0.00
NOV 97 (1)	8.81	51.38	95.41	10.00	12.98	3.20	0.82
NOV 97 (2)	9.74	37.02	99.01	7.46	11.17	1.55	2.41
DEC 97 (1)	7.00	37.79	98.38	21.76	11.47	4.64	3.27
DEC 97 (2)	5.80	23.58	98.92	2.43	8.44	3.32	5.47
DEC 97 (3)	11.40	37.15	96.33	2.43	8.98	3.46	2.38
JAN 98 (1)	11.11	26.65	97.19	9.80	9.02	8.17	2.54
JAN 98 (2)	10.20	51.47	95.13	9.29	9.16	4.65	2.04
FEB 98 (2)	18.15	59.76	88.85	9.67	6.55	16.06	11.83
FEB 98 (2)	9.76	62.63	89.96	30.37	7.98	14.74	29.95
MAR 98 (1)	17.94	43.01	89.17	31.17	7.99	22.03	39.60
MAR 98 (2)	47.79	52.95	82.01	100.00	18.26	16.31	36.71
APR 98 (1)	100.00	79.52	83.05	57.11	59.91	6.26	21.15
APR 98 (2)	76.11	100.00	95.58	10.71	100.00	6.07	9.88
MAY 98(1)	52.15	96.00	97.36	4.09	42.14	3.54	11.55
MAY 98(2)	15.87	75.33	97.80	7.33	37.24	1.75	2.80
JUN 98(1)	25.42	46.15	99.34	6.83	32.92	1.99	4.29
JUN 98(2)	11.06	26.96	99.66	0.46	41.90	1.35	0.00
JUN 98(3)	8.09	30.79	98.99	1.43	26.36	1.38	2.83
JUL 98(1)	4.76	17.19	99.62	4.37	34.29	1.99	7.00
JUL 98(2)	6.20	18.07	100.00	9.77	20.50	1.45	1.92
AUG 98(1)	2.85	11.34	99.82	10.71	15.99	0.87	2.00
AUG 98(2)	3.34	23.22	98.93	14.02	26.18	0.72	2.00
SEP 98(1)	30.29	42.51	98.99	15.64	32.01	11.37	14.41
SEP 98(2)	29.76	74.34	98.40	34.52	30.47	1.06	25.09
OCT 98(1)	10.56	57.93	96.92	9.06	24.84	74.52	3.12
OCT 98(2)	9.46	39.32	97.97	6.28	6.32	100.00	3.66
NOV 98(1)	21.77	41.71	99.46	8.36	16.11	50.38	0.39
NOV 98(2)	11.40	26.71	98.99	8.05	15.24	32.66	1.21
NOV 98(3)	8.60	30.25	97.50	5.37	16.44	73.15	0.79
DEC 98(1)	17.52	58.28	94.78	34.29	32.73	51.24	1.56
DEC 98(2)	22.07	35.27	90.43	43.63	15.09	77.70	4.70

APPENDIX B.2

Index Of Food Availability of The Forest Community For Each Phenological State Using Only The DBH Value Of The Fruiting Tree As A Measure Of Abundance. (UR = unripe fruit, HR = half ripe fruit, RF = ripe fruit).

Period	UR	HR	RF
Oct 97(1)	27.34831	46.64372	43.46361
Oct 97(2)	34.26806	38.75711	10.24745
Nov 97(1)	40.48398	74.81996	33.78097
Nov 97(2)	52.25406	75.69662	63.11082
Dec 97(1)	53.91872	60.12573	46.36116
Dec 97(2)	46.68482	48.7955	44.44503
Dec 97(3)	50.36758	48.32523	47.42014
Jan 98(1)	63.24303	59.50813	33.14088
Jan 98(2)	64.76914	69.08275	26.28613
Feb 98(1)	51.53643	96.8505	66.70693
Feb 98(2)	58.71084	96.69376	75.93462
Mar 98(1)	53.40731	100	77.8506
Mar 98(2)	52.55853	87.26406	85.20362
Apr 98(1)	57.07124	90.97112	100
Apr 98(2)	59.18482	79.1324	72.72035
May 98(1)	47.11888	49.6091	59.08044
May 98(2)	44.86401	22.98514	14.48743
Jun 98(1)	54.10126	32.96039	32.43771
Jun 98(2)	58.07303	21.50177	3.886871
Jun 98(3)	51.41428	33.0283	28.26815
Jul 98(1)	63.85225	49.34056	54.27485
Jul 98(2)	57.62995	34.17366	29.8229
Aug 98(1)	44.34242	40.77922	42.40223
Aug 98(2)	51.34661	64.6412	42.40234
Sept 98(1)	59.99392	59.04675	37.24364
Sept 98(2)	58.75235	68.68631	70.38869
Oct 98(1)	68.24052	98.54633	43.74702
Oct 98(2)	53.25812	80.41564	47.06901
Nov 98(1)	84.97585	69.8326	35.97246
Nov 98(2)	66.06004	58.44194	36.89202
Nov 98(3)	51.04241	53.78871	28.83578
Dec 98(1)	100	66.10043	40.54034
Dec 98(2)	86.7986	98.85887	60.96384

APPENDIX B.3

The Number of Individuals of each Chimpanzee Food Species Exhibiting each of the Major Phenological States in each Sample Period

a) Ripe Fruit

Species	S	S	O	O	N	N	D	D	D	J	J	F	F	M	M	A	A	M	M	J	J	J	J	J	A	A	S	S	O	O	N	N	N	D	D
BPY		1	1								2	4	1	6	3	4	1			2		1	2	1	3	3	1	2							1
CAL																								1	2	2	1								
CDU																																			
CMI																																			
COM	1	1	1																				1	1											
CSY	7	8	6																								3	4	1						
CYA												1	2	3	3	2																			
CZE																																			
FB																																			
FE								2		1	1	2	4	2		2	1																		
FM						2					1		1		2		1			1												1			
FPO							1		1							2		1	1	1													1	1	
FSA							1																								1				
FSS																	1	1																	
FSU	1				1	1	2		1			2	1	2			2	1		1			2	1						2		1			1
FVL														1																					
FVR								1	1	1	1	1	1	2	2	1	2												2	1	1	1	1	1	1
KA																																			1
LW								1	1	1																							1		
ME															1	1	1	1																	
MEX																		4	1	1							1								
MIE																		1	1	1		1	1												
MOL															2																				
MYH	1																1	3																	
OLW																																			
PSM	1																																		
Total	5	3	3	0	1	2	3	3	4	3	4	5	6	6	6	6	8	7	3	6	0	2	4	4	2	2	4	2	2	3	1	2	2	3	5

b) Half Ripe Fruit

| | | |

c) Unripe

BPY	4	3	2	5	7	8	10	8	9	7	9	6	6	6	5	5	5	6	7	7	6	6	4	4	3	2	2	3	2	4	4	8	9	6	9
CAL				2	1			1	1	1	1	2	2	2				1	3	2	2	2	5	4	2	2	3	4	5	4	5	5	4	5	5
CDU	5	5	5	5	4	2	2	1	1						7	14	18	11	10	9	11	9	10	8	7	9	10	9	7	3	5	6	6	6	5
CMI			1	2	1	2	2	1	2				2	1														1	1	1	1	1	1	8	2
COM	1	1		1											2	3	1	1	1	1	1	1				1		2	2		1	1	1	1	1
CSY	7	1																			1	1	1	1	1	2	3	1							
CYA					3	3	2	3	3	2	3	3	3	3														1	6	2	5	2	3	2	3
CZE	4	4	5	4	5	5	4	1	3	1							3	6	6	6	5	2	4	2	1	2	1								
FB																																	1	1
FE						1	2	3	2	4	6	6	6	5	3	2	1															1	2	3	3
FM					1	1	1	1	1	2	1	1	3	3	3	2	1		1	1			2	2			1		1	1	2	1	2	1	2
FPO				1	1	1	1			1			2	2	2	2	1	2	2	2	1							1	1	1	1	1	1	1	
FSA				1	1	1	1	1		1	1												1	1	2	1	1	1	1						1
FSS																1	1																		
FSU	4	4	3	4	4	4	3	2	1	5	4	4	5	6	5	4	5	2	1	4	5	4	5	3	3	5	5	6	3	2	2	4	4	5	5
FVL							1			1	1	1	1	1																		1	1	1	1
FVR							1	1	2	4	3	4	5	5	4	3	1								1	1	2	2	3	2	2	1	2	1	1
KA															1		1	2	2	2	2	2	2	1	2	1	1	1	1	1	2	1	1	1	1
LW						1	1													1	1	1	1	1		1	1	1		1	1	1	1		1
ME						2	4	4	4	4	3	2	1	1	1	1																		1	1
MEX															1	1	3	1									1							
MIE														2	2	2	2	2	1	2	2	1												
MOL													2	2	2																		1	1
MYH	1	2	1	3	2	2	3	1	3	3	3	3	3	4	2	3	3		1																
OLW			2	2	2	2	2	2	1	2	2						2		2	2								2	2	2	2	2	2	2	2
PSM	1																																		
Total	8	7	7	11	12	14	16	14	13	14	12	10	13	14	14	13	15	10	12	12	11	10	10	10	9	11	12	14	13	12	13	15	15	17	18

d) young leaves

species	S	S	O	O	N	N	D	D	J	J	F	F	M	M	A	A	M	M	J	J	J	J	J	A	A	S	S	O	O	N	N	N	D	D	D
BPY	9	6	15	14	21	21	21	21	19	17	6	8	6	5	6	12	9	6	8	7	10	13	11	9	11	8	11	13	18	21	20	20	21	19	21
CAL	1	1	1	1	0	0	0	1	0	6	5	3	6	1	2	3	2	0	0	0	1	3	0	0	2	2	2	1	1	3	2	1	1	0	1
CDU	1	2	1	2	2	5	0	1	0	0	1	0	8	13	18	20	19	16	3	3	4	0	1	0	1	1	1	1	2	0	1	1	2	1	1
CMI	5	6	19	16	15	6	6	1	2	9	16	11	3	4	4	4	1	1	1	1	0	4	1	1	3	10	14	14	12	6	2	5	5	16	7
COM	3	3	2	1	5	5	6	6	5	5	11	14	13	8	4	4	3	3	3	3	4	4	2	2	7	5	4	5	4	4	3	3	6	3	3
CSY	1	0	1	0	1	0	1	0	1	1	1	2	14	15	18	19	19	19	18	11	13	11	5	0	2	0	2	1	1	1	1	1	0	1	0
CYA	2	18	19	5	2	2	4	0	3	4	9	3	4	2	4	6	4	1	11	3	2	5	2	4	9	14	20	15	1	2	0	7	0	4	0
CZE	5	8	8	9	11	13	14	8	4	2	7	5	5	5	10	21	24	22	17	13	16	9	12	6	8	7	13	13	14	15	9	6	13	8	6
FB	0	1	2	2	2	1	2	1	1	1	1	1	1	1	1	1	2	0	0	0	0	0	0	0	0	0	1	2	2	1	0	0	1	1	0
FE	0	0	3	0	1	2	5	5	5	10	12	14	16	14	13	10	10	6	5	5	4	3	3	2	3	3	4	8	5	6	6	8	5	6	6
FM	5	6	4	5	6	7	4	5	3	1	2	3	6	5	2	2	2	0	3	2	3	3	3	4	3	5	6	3	3	4	4	4	5	3	1
FPO	0	0	0	0	1	1	1	1	1	3	2	2	2	4	2	3	2	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	2
FSA	0	0	0	1	2	1	2	2	1	2	3	3	2	3	2	1	2	1	0	0	0	0	0	0	1	1	1	1	0	1	1	1	2	1	1
FSS	0	0	1	2	4	2	3	2	1	1	4	5	1	1	1	2	1	1	1	0	0	0	1	1	1	0	0	1	1	0	0	0	2	1	5
FSU	4	5	6	7	9	9	7	7	9	8	11	15	11	13	10	6	3	1	1	0	4	2	0	1	2	1	6	8	8	8	5	5	8	14	15
FVL	0	0	1	1	1	2	2	1	1	2	2	2	2	0	0	0	0	1	0	0	0	0	1	0	0	1	1	1	1	1	2	1	1	2	1
FVR	2	4	4	6	5	10	8	8	10	9	9	11	11	13	11	11	8	4	3	4	3	5	3	4	4	5	9	9	9	10	8	8	13	6	4
KA	1	1	0	3	5	3	2	1	5	17	19	20	19	9	4	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	12	17
LW	1	0	0	0	2	3	4	4	2	1	1	3	2	2	4	4	4	4	4	3	3	1	1	2	1	0	0	1	1	0	1	1	4	1	1
ME	13	11	9	13	13	12	13	12	10	7	5	6	10	11	13	9	7	6	7	10	8	4	9	8	10	11	9	5	9	15	14	14	13	16	16
MEX	1	0	1	1	0	0	0	1	0	1	0	2	5	10	8	10	6	3	3	3	2	1	1	1	3	2	2	2	2	1	3	1	0	1	0
MIE	1	1	0	1	0	2	1	1	3	4	3	3	3	0	0	0	0	0	0	1	1	1	1	1	2	2	2	1	2	1	1	1	0	2	3
MOL	0	0	0	0	0	0	0	0	2	3	9	9	7	5	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5
MYH	14	14	12	13	17	18	18	14	16	15	15	12	12	10	9	12	6	5	8	10	8	8	11	9	11	14	18	18	16	15	14	12	15	11	9
OLW	1	1	1	1	1	3	3	3	3	3	3	2	1	0	0	0	3	2	3	3	3	3	2	3	3	3	3	3	2	3	3	3	3	1	1
PSM	0	0	4	2	1	0	0	1	1	2	10	12	13	4	1	1	2	1	0	1	0	0	0	0	0	1	0	2	5	5	3	1	1	3	7
Total	71	88	114	106	127	129	128	108	108	134	168	171	183	158	149	164	141	105	100	83	89	81	70	58	87	96	131	130	121	125	104	105	125	135	133

APPENDIX B.4

List Of Species Recorded As Fruiting In The Community-Wide Phenology Transect.

Family	Genera, Species
Anacardiaceae	Lannea welwitschii
	Pseudospondias microcarpa
Annonaceae	Cleistopholis patens
	Monodora angolensis
Apocynaceae	Funtumia africana
	Funtumia elastica
	Rauvolfia vomitoria
	Tabernaemontana holstii
Boraginaceae	Cordia millenii
	Celtis zenkeri
Cecropiaceae	Myrianthus holstii
Dichapetalaceae	Tapura fischeri
Euphorbiaceae	Antidesma laciniatum
	Croton megalocarpus
	Croton sylvaticus
	Margaritaria discoideus
	Ricinodendron heudelotii
Flacourtiaceae	Caloncoba schweinfurthii
Guttiferae	Mammea africana
Leguminosae	Albizia coriaria
	Albizia sp.
	Cynometra alexandri
	Erythrina abyssinica
	Erythrophleum suaveolens
	Mildbraediodendron excelsum
	Tetrapleura tetraptera
Meliaceae	Guarea cedrata
	Khaya anthotheca
	Trichilia prieuriana
Moraceae	Antiaris toxicaria
	Bosqueia phoberos
	Broussonetia papyrifera
	Ficus asperifolia
	Ficus barteri
	Ficus exasperata
	Ficus mucuso
	Ficus natalensis
	Ficus polita
	Ficus sansibarica
	Ficus saussureana
	Ficus sur
	Ficus vallis-choudae
	Ficus variifolia
	Milicia excelsa (Chlorophora)
	Morus Lactea
Myrtaceae	Psidium guajava
Palmae	Raphia farinifera

APPENDIX B.4 contd.

Oleaceae	Olea welwitschii
Rhamnaceae	Maesopsis eminii
Rubiaceae	Belonophora hypoglauca
	Dictyandra arborescens
Sapindaceae	Majidea fosteri
Sapotaceae	Chrysophyllum albidum
	Chrysophyllum gorungosanum
	Chrysophyllum perpulchrum
Simaroubaceae	Irvingia gabonensis
Tiliaceae	Desplatsia chrysochlamys
	Desplatsia dewevrei
	Glyphaea brevis
Ulmaceae	Celtis durandii
	Celtis mildbraedii
	Celtis wightii
Violaceae	Rinorea ardisiaeflora
Unknown (climber)	Alaphia sp.

APPENDIX B.5

List Of The Dates Of The Two Weekly Phenology Periods. The Phenology Sampling Was Carried Out On The First Three Days Of Each Period.

Phenology Period	Dates
Sep 97 (1)	08/09 - 21/09/97
Sep 97 (2)	22/09 - 02/10/97
Oct 97 (1)	06/10 - 19/10/97
Oct 97 (2)	20/10 - 02/11/97
Nov 97 (1)	03/11 - 16/11/97
Nov 97 (2)	17/11 - 30/11/97
Dec 97 (1)	01/12 - 14/12/97
Dec 97 (2)	15/12 - 28/12/97
Dec 97 (3)	29/12/97 - 11/01/98
Jan 98 (1)	12/01 - 25/01/98
Jan 98 (2)	25/01 - 08/02/98
Feb 98 (1)	09/02 - 22/02/98
Feb 98 (2)	23/02 - 08/04/98
Mar 98 (1)	09/03 - 22/03/98
Mar 98 (2)	23/03 - 05/04/98
Apr 98 (1)	06/04 - 19/04/98
Apr 98 (2)	20/04 - 03/05/98
May 98 (1)	04/05 - 17/05/98
May 98 (2)	18/05 - 31/05/98
Jun 98 (1)	01/06 - 14/06/98
Jun 98 (2)	15/06 - 28/06/98
Jun 98 (3)	29/06 - 12/07/98
Jul 98 (1)	13/07 - 26/07/98
Jul 98 (2)	27/07 - 09/07/98
Aug 98 (1)	10/08 - 23/08/98
Aug 98 (2)	24/08 - 06/09/98
Sep 98 (1)	07/09 - 20/09/98
Sep 98 (2)	21/09 - 04/10/98
Oct 98 (1)	05/10 - 18/10/98
Oct 98 (2)	19/10 - 01/11/98
Nov 98 (1)	02/11 - 15/11/98
Nov 98 (2)	16/11 - 29/11/98
Nov 98 (3)	30/11 - 13/12/98
Dec 98 (1)	14/12 - 27/12/98
Dec 98 (2)	28/12/98 - 10/01/99

APPENDIX C.1

The Number of Activity Budget Scans for each Individual.

Individual	Apr(1)	Apr(2)	Aug(1)	Aug(2)	Dec(3)	Feb(1)	Feb(2)	Jan(1)	Jan(2)	Jul(1)	Jul(2)	Jun(1)	Jun(2)	Jun(3)	Mar(1)	Mar(2)	May(1)	May(2)	Nov(1)	Nov(2)	Nov(3)	Oct(1)	Oct(2)	Sep(1)	Sep(2)	Total
AY	36	67	38	23	13	7	14	23	7	9	55	19	22	2	43	39	49	8	65	6	31	25	59	17	41	718
BB	12	38	42	17	0	6	21	31	3	2	36	13	3	0	14	14	23	8	41	13	21	35	38	30	8	469
BK	31	60	32	7	6	17	10	28	10	7	30	3	9	4	35	19	13	5	55	5	23	15	40	27	47	538
BN	9	0	0	0	0	0	21	0	9	0	0	0	0	7	13	43	4	2	27	6	9	0	24	0	8	182
BY	33	37	0	0	0	42	12	31	5	0	19	0	5	1	40	25	26	3	70	3	27	13	25	2	29	448
CL	26	45	23	20	0	12	6	21	8	21	2	3	20	4	28	12	18	22	36	11	34	83	44	32	44	575
DN	42	54	28	28	13	40	16	34	5	33	27	0	4	4	35	53	43	11	70	14	34	25	51	35	69	768
EM	3	4	14	1	0	2	6	0	0	0	13	0	11	3	16	0	22	7	17	12	4	25	21	11	11	203
GS	18	29	23	22	6	13	7	17	0	2	18	13	23	6	41	32	28	2	38	18	12	20	41	5	23	457
HT	0	29	0	14	10	0	0	0	0	0	0	0	0	0	1	0	0	0	12	14	3	0	20	10	0	113
JM	16	15	29	0	5	38	5	14	2	2	19	9	9	0	13	1	41	0	47	5	13	9	39	12	24	367
JN	33	33	51	26	19	20	15	53	14	15	7	16	4	5	23	38	32	50	63	8	28	40	67	37	85	782
JN	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
KG	22	24	15	14	8	0	15	45	0	0	1	0	1	0	11	13	10	41	15	0	0	56	20	0	28	339
KK	33	50	0	0	5	43	24	25	15	0	0	14	12	9	61	41	48	41	0	0	0	0	0	0	0	421
KL	11	71	39	21	4	0	5	14	0	0	67	2	20	4	14	21	15	0	19	15	11	19	15	12	2	401
KU	29	44	20	8	18	12	4	5	8	11	11	23	19	4	45	28	12	3	9	6	13	44	26	26	16	444
KW	16	47	54	26	0	11	50	0	4	9	59	7	8	8	25	32	17	17	20	6	0	54	52	0	6	528
KY	34	26	36	24	27	5	16	30	22	11	49	2	5	1	27	45	23	49	24	0	0	61	17	11	11	556
MA	13	96	18	0	24	17	13	17	0	25	11	17	20	4	44	35	36	31	72	14	41	32	56	13	33	682
MG	37	72	38	37	4	35	14	37	1	16	20	19	31	5	53	45	44	19	39	7	4	31	51	21	23	703
MK	13	52	26	6	0	12	25	41	0	0	6	0	1	3	4	42	46	8	17	17	0	43	59	0	0	421
MM	0	0	16	0	0	3	0	0	0	0	3	0	0	4	3	20	0	0	0	0	0	0	0	0	0	49
MU	17	45	15	6	0	6	9	9	1	13	16	19	20	9	26	39	39	8	43	18	12	6	19	15	24	434
NB	21	49	42	16	8	16	1	10	4	15	45	8	27	8	52	39	48	7	17	38	18	9	45	42	22	607
NJ	30	34	3	9	14	35	21	17	8	8	6	26	14	2	35	34	27	13	38	6	12	23	54	0	50	519
NK	30	35	28	0	0	8	17	32	17	0	23	4	2	9	50	21	31	17	44	14	21	1	70	13	56	543
RD	9	45	4	8	0	3	9	0	0	0	5	3	7	5	0	0	14	25	9	6	0	12	6	0	5	175
RH	8	53	0	0	0	2	19	0	9	0	0	0	2	3	25	17	19	13	0	17	13	0	59	0	0	259
SR	26	19	3	0	0	9	10	0	5	0	0	0	0	0	61	16	21	0	26	19	15	28	21	0	0	279
TK	33	38	23	3	0	8	1	18	0	2	18	19	3	1	30	21	20	0	58	10	17	8	31	7	52	421
VN	25	1	36	7	18	20	3	27	7	28	33	1	11	0	21	34	11	2	66	5	20	11	37	21	31	476
VT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	8	0	27	0	7	0	0	0	0	0	46
ZA	8	20	9	11	0	17	18	1	0	0	44	0	0	0	2	14	23	36	8	0	6	0	13	20	0	250
ZF	7	30	14	9	0	2	2	0	10	0	37	0	13	7	1	8	35	16	18	4	28	17	31	8	57	354
ZM	9	52	58	15	19	0	26	0	3	17	74	2	9	3	16	17	34	39	24	0	0	34	28	17	13	509
ZT	25	40	24	14	17	25	7	31	0	1	25	15	10	4	47	43	22	24	20	0	0	37	54	18	46	549
	715	1354	801	392	238	486	442	612	177	247	779	257	345	129	959	909	895	554	1127	324	470	816	1233	462	864	15587

APPENDIX C.2

The Number of Scans of Feeding Behaviour for each Individual.

Individual	Dec(3)	Jan(1)	Jan(2)	Feb(1)	Feb(2)	Mar(1)	Mar(2)	Apr(1)	Apr(2)	May(1)	May(2)	Jun(1)	Jun(2)	Jun(3)	Jul(1)	Jul(2)	Aug(1)	Aug(2)	Sep(1)	Sep(2)	Oct(1)	Oct(2)	Nov(1)	Nov(2)	Nov(3)	Total
AY	10	12	5	3	7	21	20	19	47	20	5	8	9	1	6	21	18	7	7	22	12	36	16	3	15	350
BB	0	18	1	4	3	7	11	4	32	15	6	6	2	0	1	19	26	9	16	6	26	21	14	10	10	267
BK	3	17	9	7	5	18	8	16	51	7	4	1	2	3	1	7	24	6	11	19	2	17	17	3	12	270
BN	0	0	4	0	9	10	38	1	0	2	1	0	0	4	0	0	0	0	0	6	0	19	11	5	3	113
BY	0	16	5	14	7	15	21	13	27	7	2	0	3	0	0	7	0	0	0	19	3	12	22	0	6	199
CL	0	13	5	9	2	13	5	16	36	13	18	2	11	1	7	0	14	14	13	19	44	32	20	6	20	333
DN	4	13	4	14	8	10	30	15	31	19	4	0	1	0	11	4	3	5	8	25	7	24	21	3	12	276
EM	0	0	0	1	0	3	0	2	0	12	3	0	6	2	0	7	12	0	5	3	15	11	10	9	4	105
GS	5	8	0	5	2	17	15	2	20	19	2	3	15	3	1	10	12	7	0	16	15	24	19	11	6	237
HT	6	0	0	0	0	1	0	0	27	0	0	0	0	0	0	0	0	3	2	0	0	15	10	6	3	73
JM	4	6	2	15	4	6	1	11	10	26	0	3	0	0	1	2	18	0	2	10	3	22	14	1	1	162
JN	9	31	8	12	8	16	22	21	17	16	26	8	2	2	3	2	30	18	20	38	24	31	17	3	14	398
KG	6	13	0	0	10	6	10	14	22	4	14	0	0	0	0	1	2	2	0	12	18	8	9	0	0	151
KK	3	16	7	14	12	30	28	10	38	27	10	4	9	3	0	0	0	0	0	0	0	0	0	0	0	211
KL	3	9	0	0	4	8	17	9	60	8	0	1	13	4	0	35	20	8	3	1	9	9	17	6	9	253
KU	11	0	5	8	1	20	16	12	35	8	2	11	8	3	2	6	8	4	3	7	32	17	2	4	7	232
KW	0	0	3	6	26	23	21	13	40	15	7	4	7	6	3	43	23	14	0	6	34	34	12	1	0	341
KY	17	13	16	3	8	16	30	17	18	12	20	1	3	0	4	25	14	11	6	5	35	12	6	0	0	292
MA	12	7	0	4	7	14	20	10	68	14	21	9	9	3	6	6	3	0	1	13	23	37	15	4	15	321
MG	4	11	1	10	4	22	37	20	42	24	9	3	19	2	6	6	10	14	5	12	23	28	17	5	1	335
MK	0	21	0	4	10	2	20	3	36	14	6	0	0	0	0	0	15	2	0	0	17	21	12	5	0	188
MM	0	0	0	0	0	2	12	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	21
MU	0	6	1	3	5	15	25	6	41	24	8	10	12	4	3	10	11	3	3	10	2	13	10	8	6	239
NB	5	5	1	9	0	37	23	13	32	24	5	5	19	2	1	21	13	8	19	12	4	17	10	10	11	306
NJ	4	9	5	14	14	16	21	10	18	16	6	10	6	0	1	1	0	0	0	16	16	33	14	4	3	237
NK	0	18	9	7	9	35	15	18	25	19	6	4	2	4	0	9	13	0	0	27	0	43	15	9	15	302
RD	0	0	0	3	3	0	0	9	33	7	15	3	4	5	0	3	1	7	0	3	6	4	1	1	0	108
RH	0	0	8	2	9	12	10	5	30	8	4	0	2	0	0	0	0	0	0	0	0	30	0	11	9	140
SR	0	0	2	4	4	32	12	20	15	3	0	0	0	0	0	0	2	0	0	0	13	12	10	14	10	153
TK	0	7	0	1	0	18	15	22	32	15	0	13	3	0	2	8	10	2	4	27	8	22	15	7	9	240
VN	10	9	3	6	1	8	21	16	1	5	1	1	2	0	8	14	13	5	4	18	6	24	24	1	10	211
VT	0	0	0	0	0	2	4	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	2	0	18
ZA	0	1	0	10	10	1	13	7	18	12	24	0	0	0	0	17	5	3	8	0	0	4	5	0	4	142
ZF	0	0	5	1	2	0	4	4	14	16	10	0	7	3	0	15	3	4	2	30	11	19	7	4	16	177
ZM	8	0	1	0	6	10	13	0	33	16	12	0	6	1	6	16	21	4	6	9	13	21	7	0	0	209
ZT	8	11	0	8	4	25	30	11	25	10	16	4	5	2	0	9	9	9	7	17	24	22	7	0	0	263
Total	132	290	110	201	204	491	588	369	974	458	277	114	187	58	73	324	360	169	155	408	445	694	406	156	231	7874

APPENDIX C.3

Proportion of Time Spent Feeding on Different Food Species in each Period.

	Dec(3)	Jan(1)	Jan(2)	Feb(1)	Feb(2)	Mar(1)	Mar(2)	Apr(1)	Apr(2)	May(1)	May(2)	Jun(1)	Jun(2)	Jun(3)	Jul(1)	Jul(2)	Aug(1)	Aug(2)	Sep(1)	Sep(2)	Oct(1)	Oct(2)	Nov(1)	Nov(2)	Nov(3)	Total
AFR	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.004	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
ALP	0.000	0.000	0.027	0.000	0.029	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.047	0.000	0.152	0.008
ANT	0.000	0.000	0.000	0.000	0.005	0.000	0.026	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003
BD	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.032	0.000	0.000	0.000	0.000	0.043	0.003
BPY	0.000	0.066	0.000	0.020	0.000	0.012	0.000	0.000	0.031	0.247	0.000	0.114	0.037	0.000	0.068	0.231	0.281	0.243	0.000	0.000	0.737	0.797	0.429	0.519	0.065	0.199
CAL	0.000	0.000	0.000	0.010	0.000	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
CGO	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.048	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.074	0.003
CLM	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
CLP	0.000	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.001
CMI	0.144	0.197	0.391	0.214	0.015	0.002	0.000	0.000	0.000	0.002	0.000	0.000	0.016	0.241	0.082	0.000	0.158	0.024	0.316	0.386	0.002	0.000	0.002	0.006	0.485	0.073
COM	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.067	0.065	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005
CPR	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.048	0.138	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
CWI	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.039	0.142	0.002	0.000	0.000	0.000	0.000	0.009
CYA	0.000	0.024	0.073	0.129	0.250	0.458	0.206	0.171	0.000	0.024	0.004	0.842	0.743	0.621	0.397	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000	0.000	0.104
CZE	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.038	0.055	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.009
DD	0.023	0.000	0.000	0.005	0.000	0.000	0.000	0.070	0.001	0.009	0.000	0.000	0.000	0.000	0.068	0.000	0.000	0.000	0.006	0.007	0.000	0.000	0.000	0.000	0.004	0.006
DEX	0.000	0.000	0.000	0.000	0.000	0.045	0.027	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005
FO	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
FB	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.097	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003
FBR	0.682	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011
FE	0.008	0.328	0.091	0.010	0.044	0.006	0.014	0.049	0.007	0.002	0.032	0.000	0.000	0.000	0.027	0.015	0.000	0.000	0.000	0.000	0.013	0.055	0.261	0.077	0.000	0.042
FM	0.000	0.179	0.000	0.010	0.010	0.000	0.692	0.027	0.748	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.154	0.130	0.160
FN	0.000	0.000	0.000	0.030	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.037	0.000	0.000	0.003
FPO	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.001
FSA	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.166	0.000	0.027	0.000	0.000	0.000	0.011
FSS	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.059	0.000	0.022	0.000	0.001	0.017	0.000	0.000	0.004
FSU	0.000	0.121	0.055	0.234	0.520	0.318	0.034	0.645	0.163	0.504	0.520	0.044	0.021	0.000	0.096	0.750	0.336	0.509	0.523	0.200	0.222	0.101	0.200	0.019	0.048	0.258
FVL	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.032	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
FVR	0.015	0.021	0.000	0.000	0.000	0.002	0.000	0.003	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.111	0.000	0.000	0.007	0.018	0.004	0.000	0.224	0.000	0.013
FW	0.000	0.000	0.000	0.000	0.044	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
KA	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.002	0.002	0.004	0.000	0.000	0.000	0.001
LPT	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LM	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LW	0.000	0.052	0.000	0.000	0.034	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003
MEX	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.002	0.054	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
MIE	0.000	0.000	0.000	0.000	0.049	0.000	0.000	0.000	0.009	0.109	0.101	0.000	0.070	0.000	0.233	0.000	0.042	0.053	0.103	0.000	0.000	0.000	0.000	0.000	0.000	0.021
MOL	0.000	0.000	0.000	0.000	0.000	0.132	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.008
MYH	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.119	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.004
RF	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001
TRD	0.000	0.000	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
TC	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.003	0.000	0.000	0.004	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.001
UCA	0.121	0.000	0.364	0.308	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.027	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.016
?	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.001

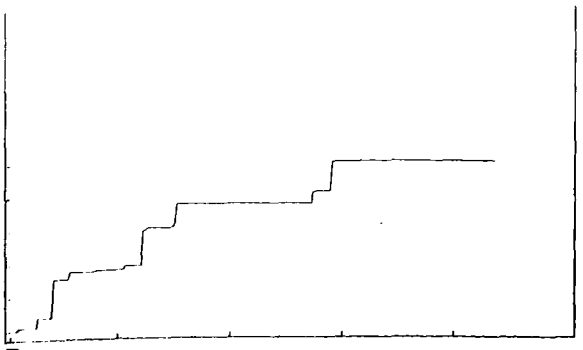
APPENDIX C.4

Time Spent Feeding on Different Food Items in each Phenology Period.

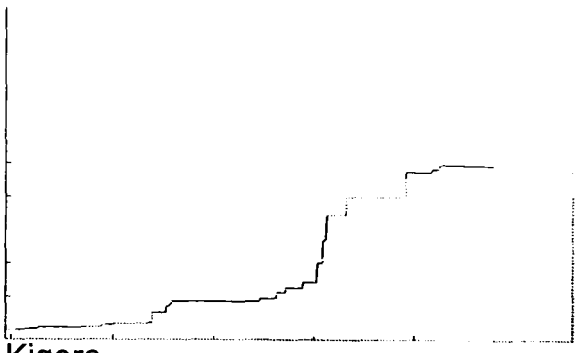
FOOD ITEM	Dec(3)	Jan(1)	Jan(2)	Feb(1)	Feb(2)	Mar(1)	Mar(2)	Apr(1)	Apr(2)	May(1)	May(2)	Jun(1)	Jun(2)	Jun(3)	Jul(1)	Jul(2)	Aug(1)	Aug(2)	Sep(1)	Sep(2)	Oct(1)	Oct(2)	Nov(1)	Nov(2)	Nov(3)
?	0.000	0.004	0.018	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
BARK	0.008	0.025	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.029	0.004	0.000	0.000	0.034	0.000	0.000	0.006	0.000	0.000	0.025	0.002	0.010	0.020	0.000	0.000
BD/YL	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
BU	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.248	0.006	0.000	0.000	0.000
FL	0.235	0.105	0.618	0.348	0.000	0.000	0.000	0.000	0.000	0.035	0.000	0.000	0.000	0.000	0.027	0.000	0.000	0.000	0.000	0.002	0.243	0.663	0.300	0.462	0.229
FL/BU	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000
FL/UR	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
HR	0.000	0.000	0.000	0.032	0.229	0.003	0.031	0.261	0.051	0.196	0.062	0.000	0.000	0.000	0.000	0.012	0.017	0.142	0.181	0.000	0.105	0.040	0.020	0.000	0.000
PITH	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.016	0.000	0.000	0.014	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
RF	0.674	0.054	0.009	0.037	0.337	0.575	0.750	0.473	0.856	0.366	0.659	0.000	0.194	0.138	0.411	0.836	0.669	0.654	0.329	0.206	0.085	0.028	0.128	0.167	0.294
RF/UR	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.043	0.000	0.000	0.000	0.000	0.000	0.000	0.000
RW	0.000	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SE	0.000	0.000	0.055	0.128	0.177	0.344	0.206	0.171	0.000	0.000	0.004	0.842	0.747	0.586	0.397	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
UR	0.030	0.656	0.164	0.193	0.200	0.056	0.014	0.079	0.017	0.106	0.207	0.079	0.000	0.000	0.027	0.117	0.022	0.074	0.129	0.233	0.083	0.123	0.405	0.308	0.156
YL	0.023	0.127	0.118	0.257	0.057	0.020	0.000	0.000	0.070	0.269	0.033	0.079	0.048	0.241	0.137	0.034	0.286	0.086	0.355	0.514	0.234	0.127	0.128	0.064	0.320
YL/FL	0.030	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.020	0.000	0.000	0.000	0.000	0.000
Grand Total	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

APPENDIX D.1

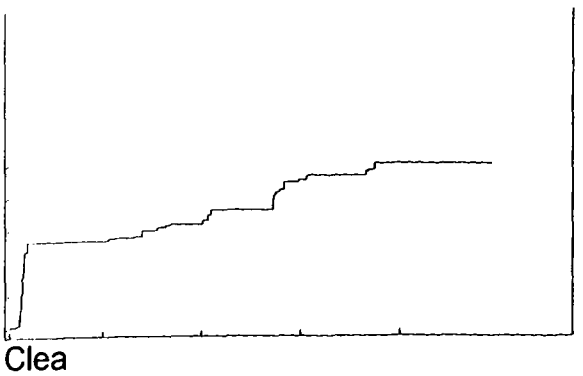
Graphs Showing The Relationship Between Number Of Observations And The Percentage Of Range Size For All Individual Females (*y axis = the percentage of home range, x axis = the number of observations).*



Banura

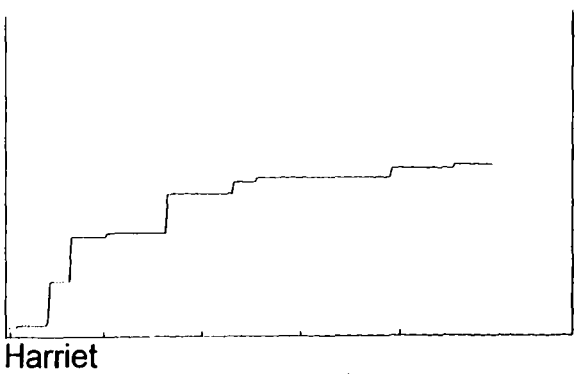


Kigere

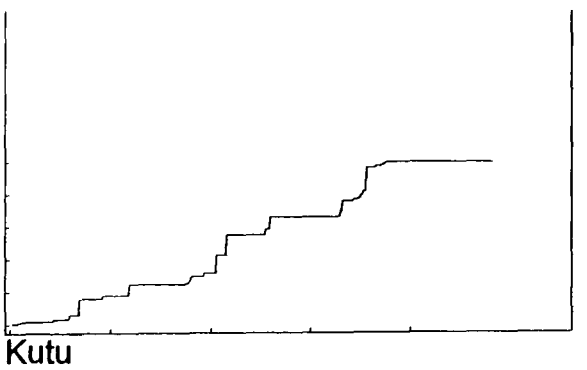


Clea

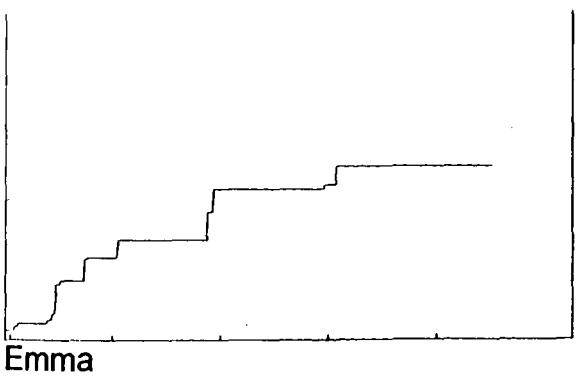
Kalema



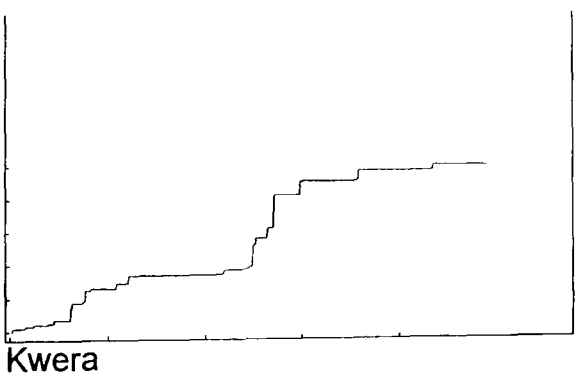
Harriet



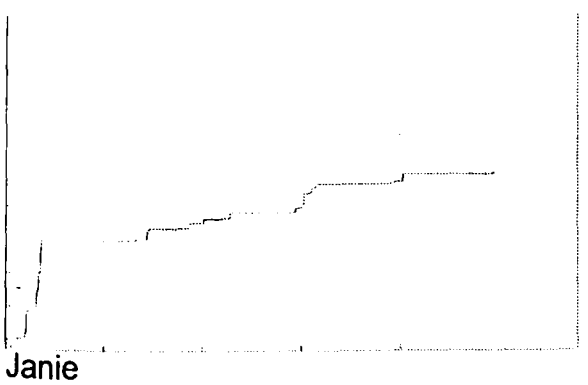
Kutu



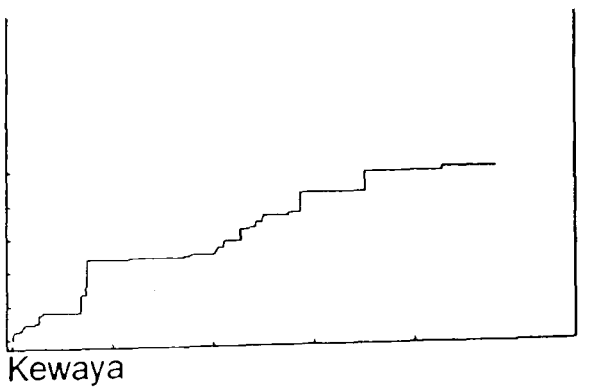
Emma



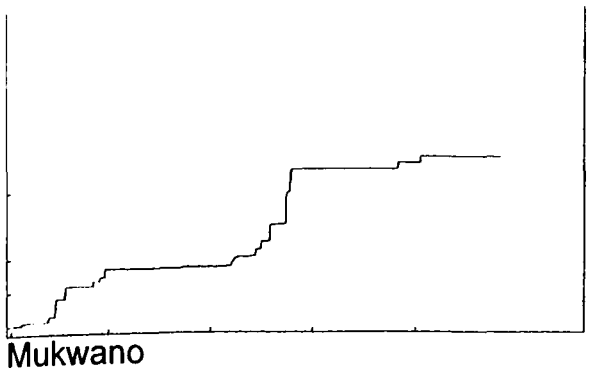
Kwera

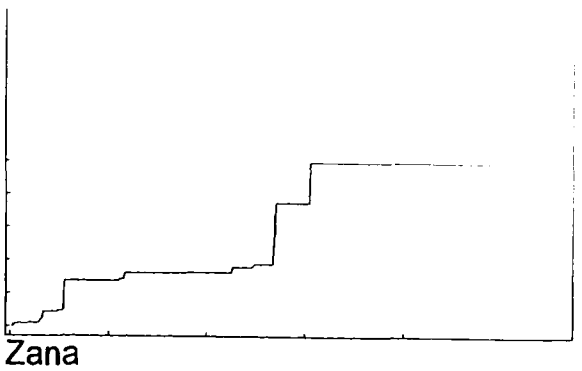


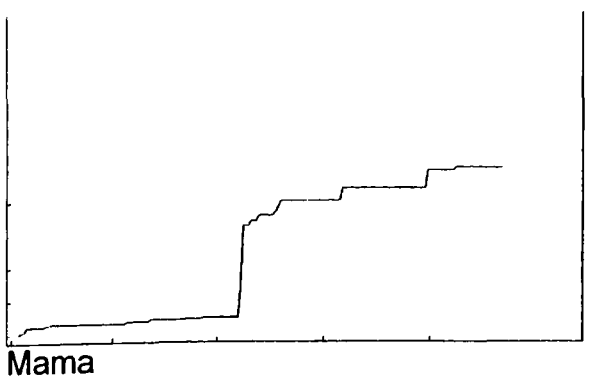
Janie

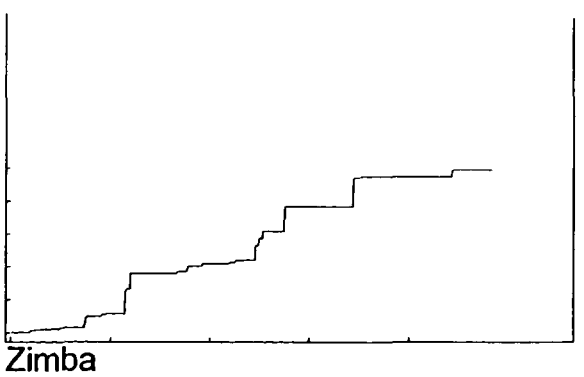


Kewaya


Mukwano


Zana


Mama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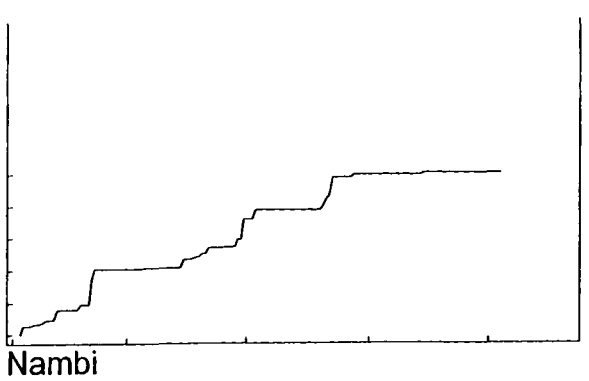
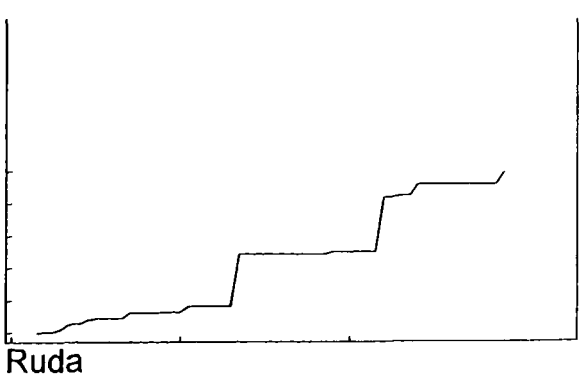
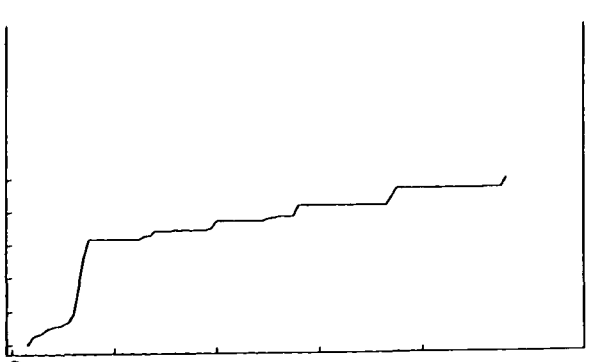
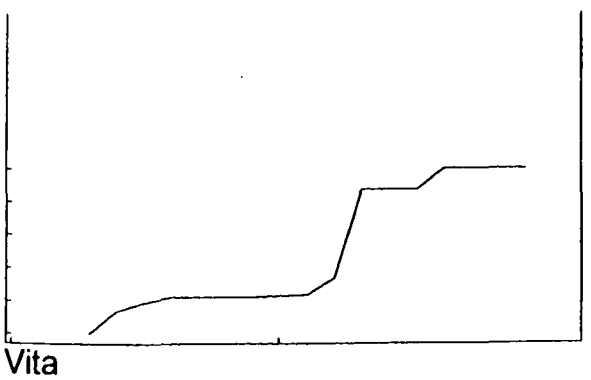

Nambi


Ruda

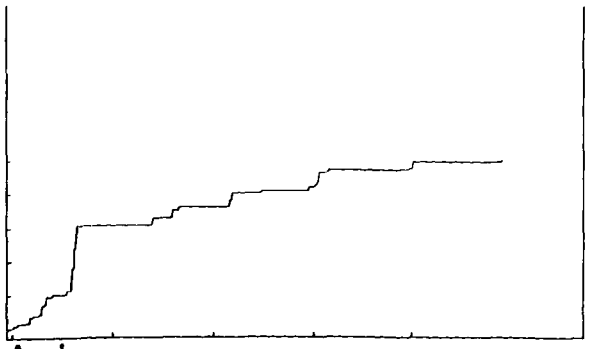

Ruhara


Sara

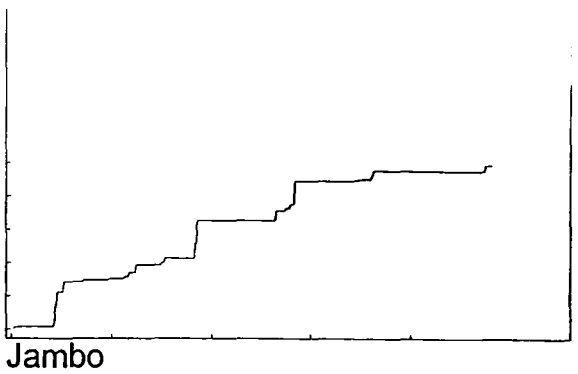

Vita

APPENDIX D.2

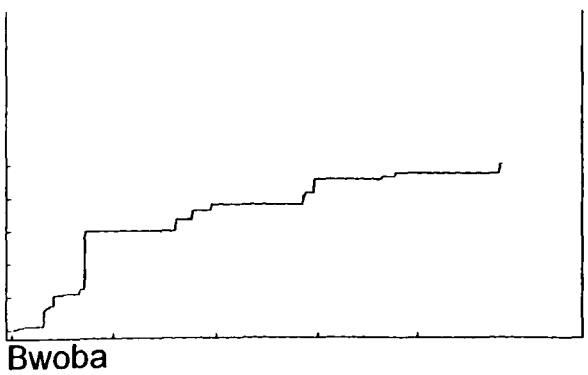
Graphs of relationships between the number of observations and range size for all males *(y axis = percentage of home range, x axis = the number of observations).*



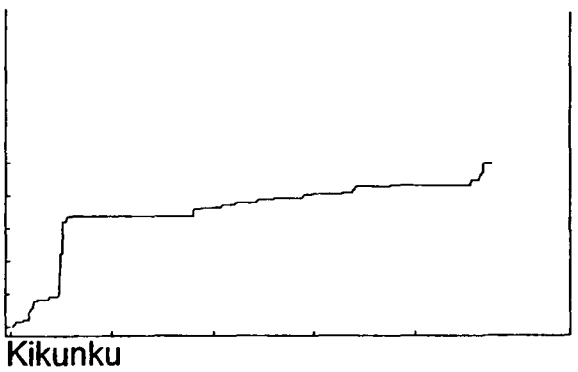
Andy



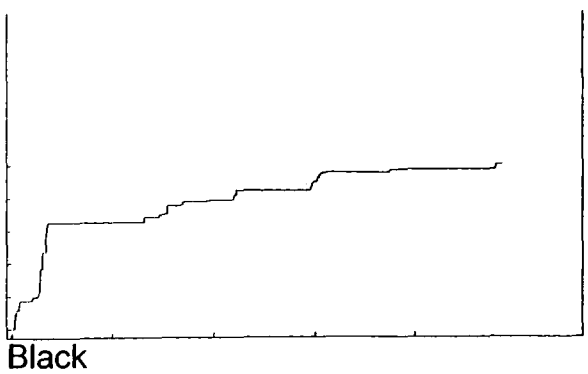
Jambo



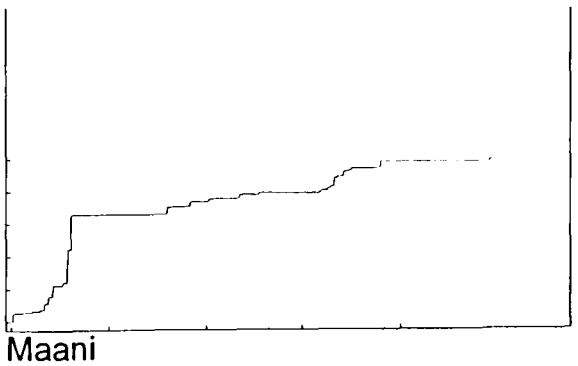
Bwoba



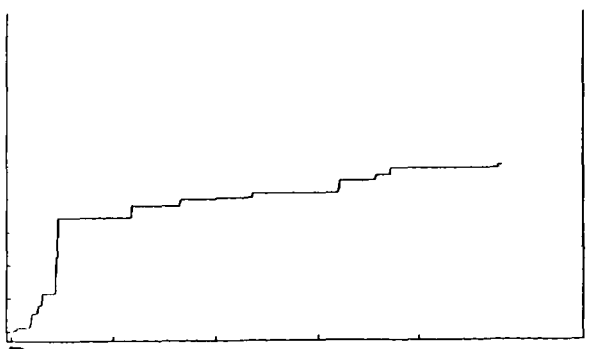
Kikunku



Black

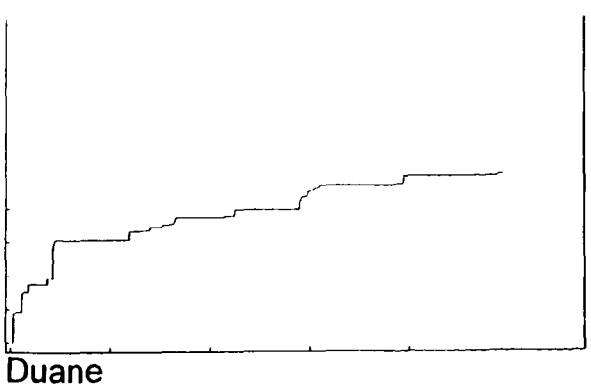


Maani

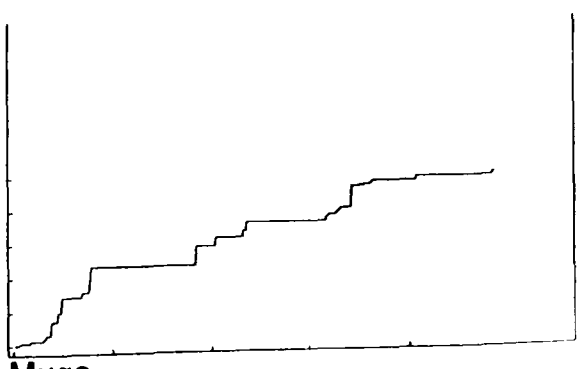


Bwoya

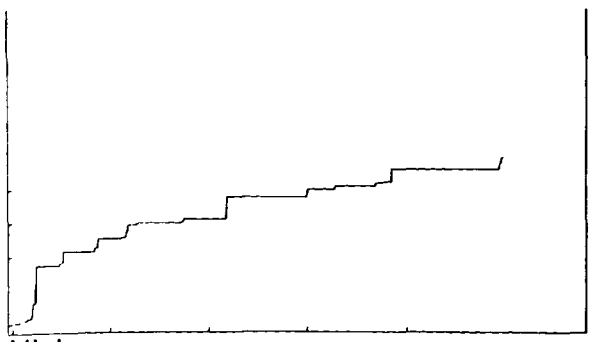
Magosi

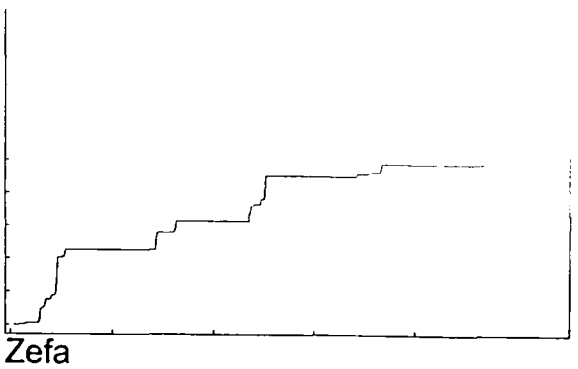


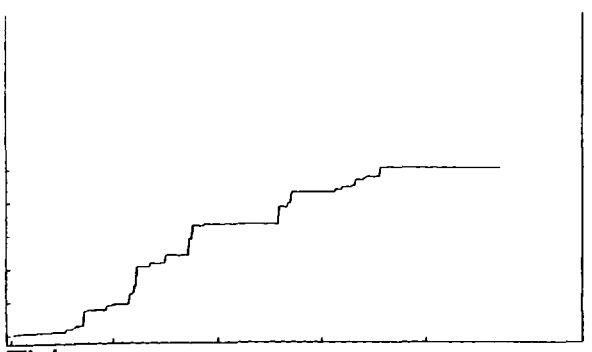
Duane

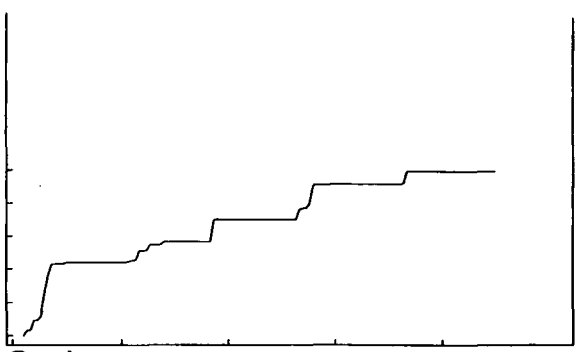


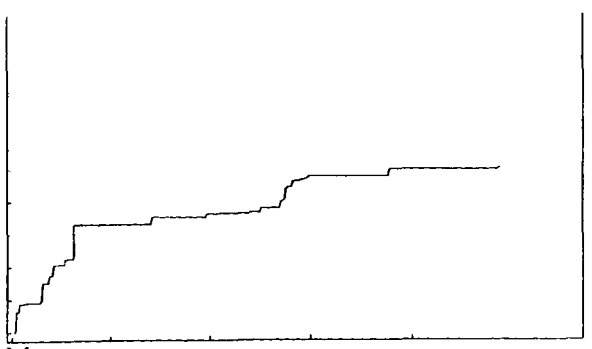
Muga

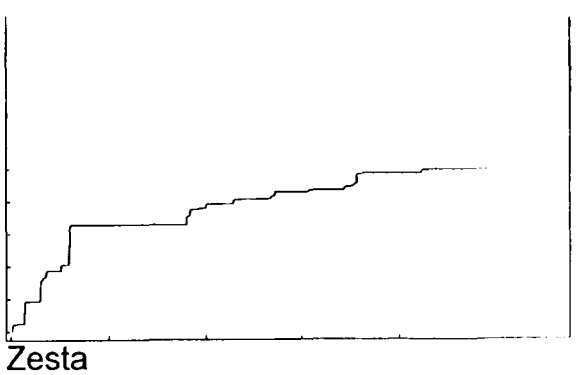

Nick


Zefa


Tinka

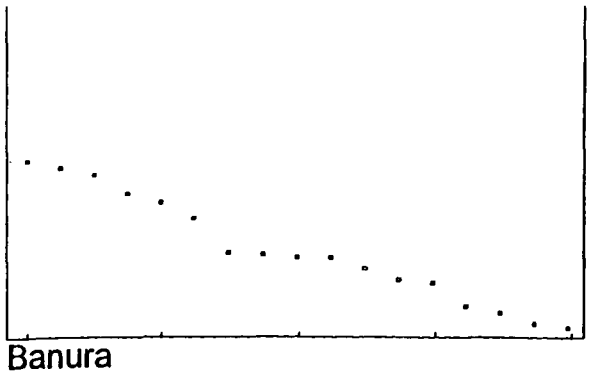

Gashom


Vernon

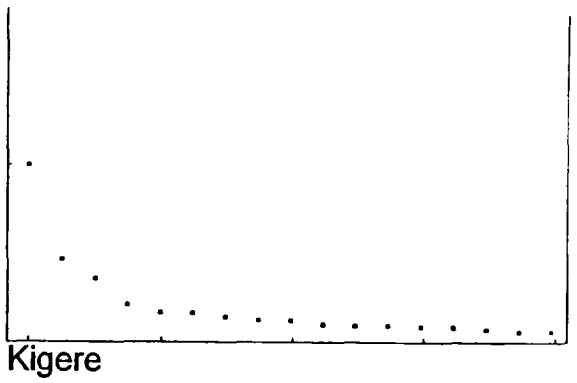

Zesta

APPENDIX D.3

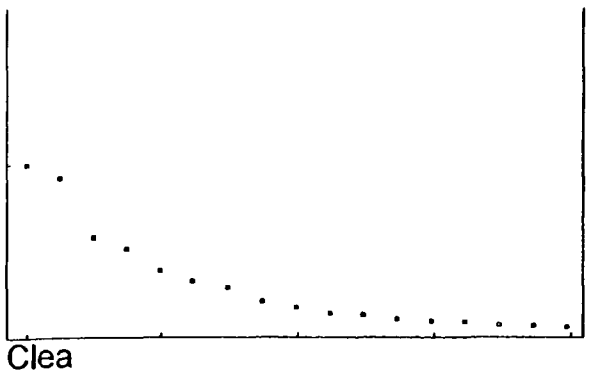
Graphs showing patterns of utilisation of range area for individual females. *(y axis = the percentage of home range, x axis =the percentage of observations, reverse scale 100 - 0).*



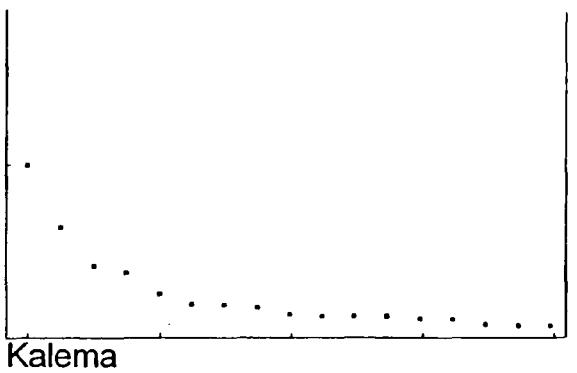
Banura



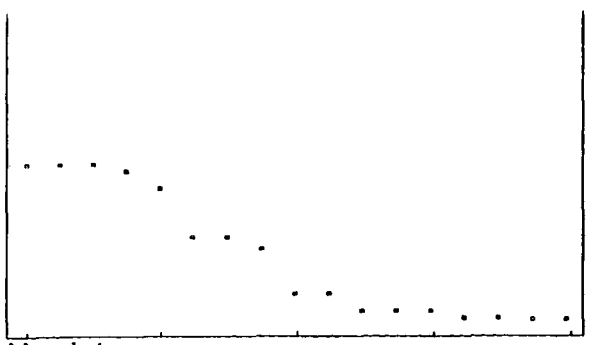
Kigere



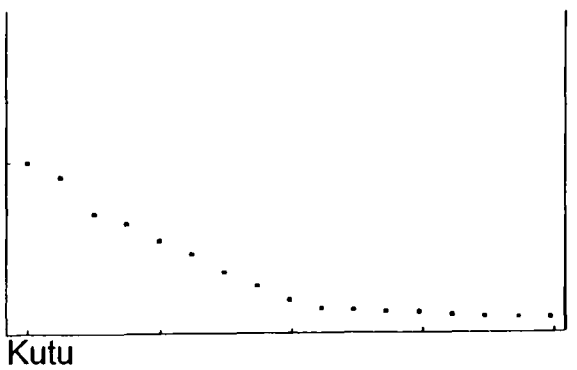
Clea



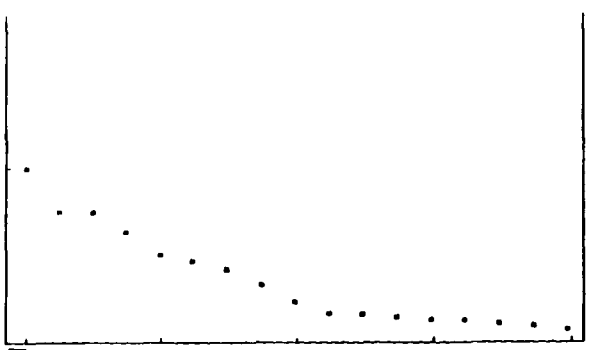
Kalema



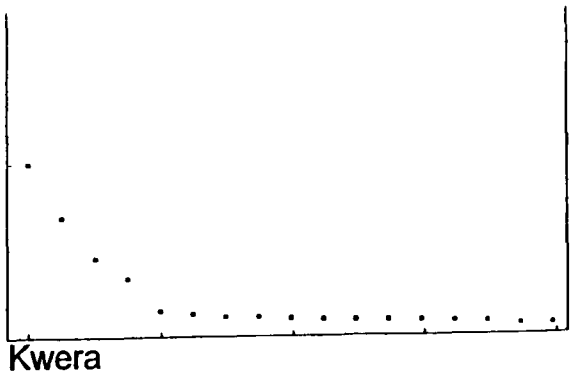
Harriet



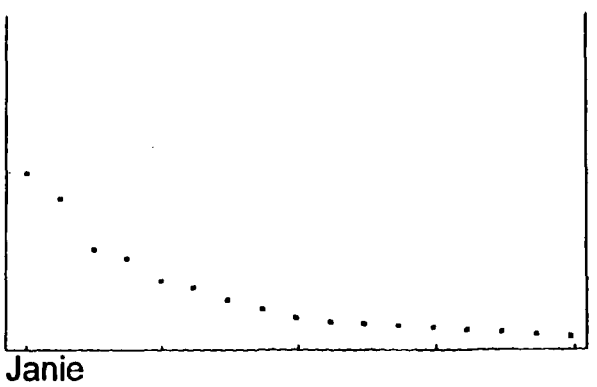
Kutu



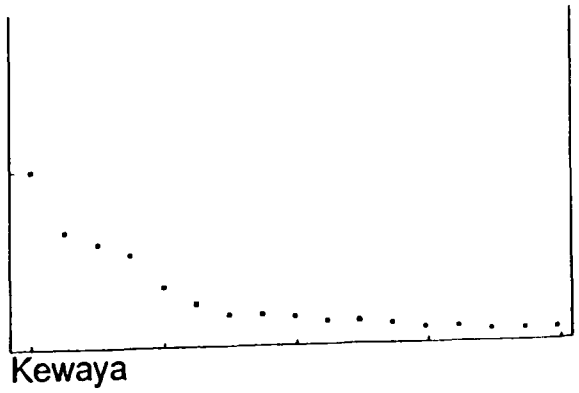
Emma



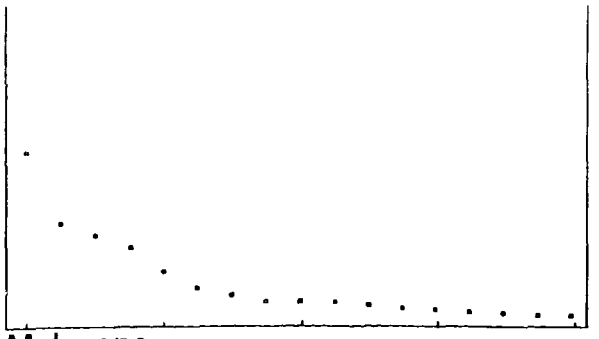
Kwera

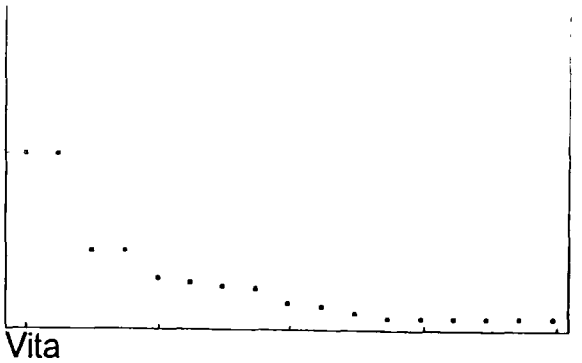


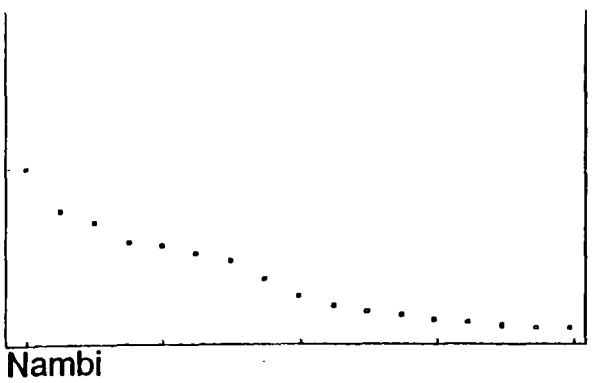
Janie

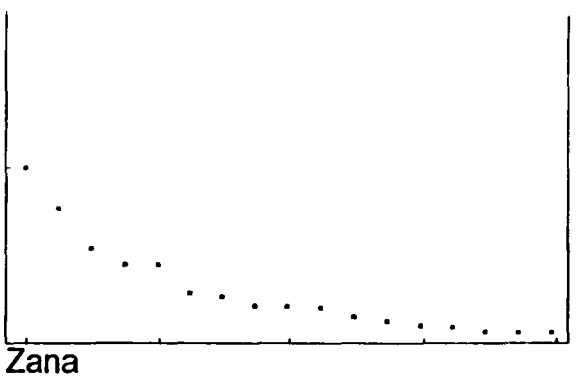


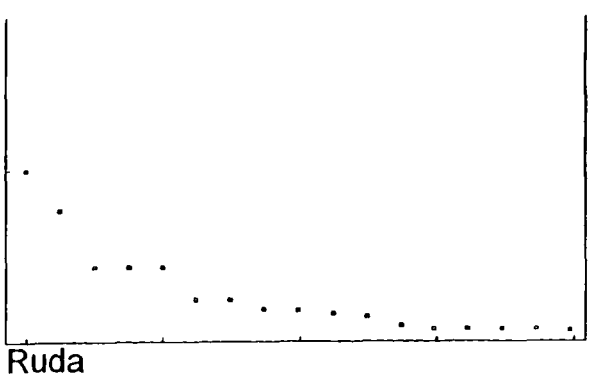
Kewaya

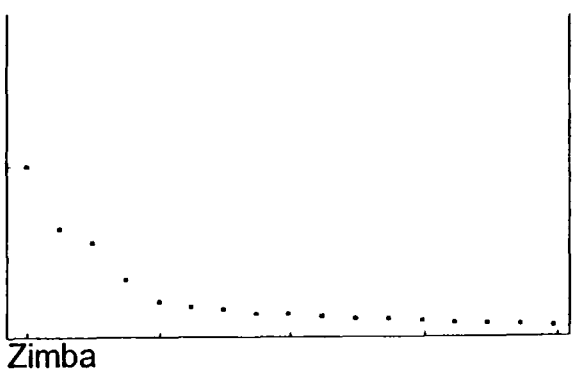

Mukwano

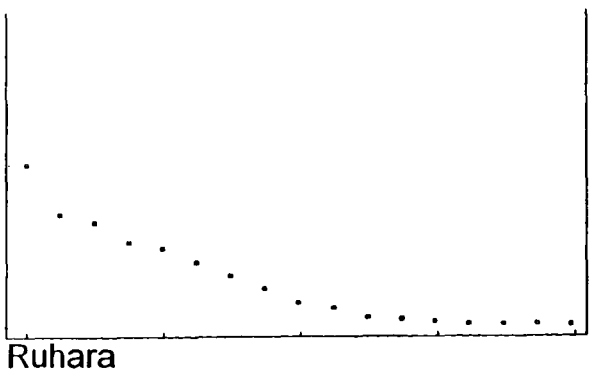

Vita

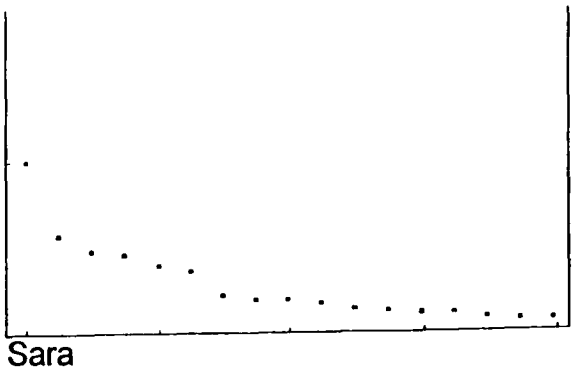

Nambi

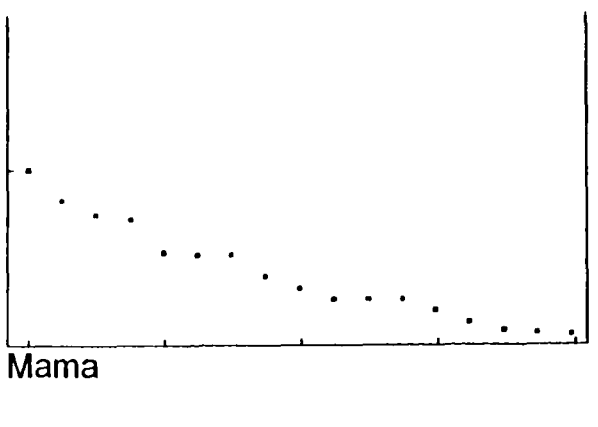

Zana


Ruda


Zimba


Ruhara


Sara


Mama

APPENDIX E.1

Dyadic Association Indices During the Whole Study Perod, (January 1998- December 1998)

SCAN	AY	BB	BK	BN	BY	CL	DN	GS	HT	EM	JM	JN	KG	KK	KL	KU	KW	KY	MA	MG	MK	MM	MU	NB	NJ	NK	RD	RH	SR	TK	VN	VT	ZA	ZF	ZM	ZT
AY																																				
BB	0.16																																			
BK	0.19	0.14																																		
BN	0.05	0.06	0.05																																	
BY	0.16	0.13	0.17	0.07																																
CL	0.16	0.14	0.16	0.04	0.11																															
DN	0.18	0.13	0.18	0.06	0.18	0.15																														
GS	0.16	0.14	0.14	0.05	0.14	0.13	0.12																													
HT	0.03	0.03	0.06	0.02	0.03	0.04	0.03	0.01																												
EM	0.08	0.07	0.06	0.02	0.07	0.07	0.08	0.08	0.01																											
JM	0.12	0.08	0.13	0.03	0.14	0.10	0.14	0.11	0.02	0.09																										
JN	0.19	0.15	0.18	0.05	0.15	0.19	0.19	0.15	0.04	0.06	0.12																									
KG	0.09	0.11	0.09	0.04	0.07	0.10	0.08	0.10	0.04	0.04	0.05	0.11																								
KK	0.13	0.11	0.15	0.06	0.15	0.11	0.16	0.14	0.02	0.06	0.11	0.14	0.11																							
KL	0.13	0.13	0.10	0.05	0.08	0.08	0.10	0.09	0.08	0.04	0.06	0.10	0.13	0.09																						
KU	0.17	0.14	0.16	0.09	0.13	0.14	0.12	0.13	0.10	0.05	0.13	0.15	0.12	0.14	0.15																					
KW	0.14	0.16	0.10	0.07	0.11	0.11	0.12	0.10	0.04	0.05	0.07	0.13	0.11	0.13	0.15	0.15																				
KY	0.12	0.13	0.11	0.06	0.10	0.11	0.13	0.08	0.05	0.05	0.06	0.14	0.08	0.13	0.11	0.11	0.15																			
MA	0.19	0.15	0.18	0.05	0.15	0.16	0.20	0.16	0.04	0.08	0.12	0.19	0.09	0.16	0.09	0.15	0.12	0.11																		
MG	0.16	0.15	0.15	0.05	0.17	0.12	0.18	0.16	0.02	0.08	0.11	0.14	0.08	0.14	0.09	0.13	0.11	0.10	0.17																	
MK	0.12	0.13	0.14	0.06	0.11	0.12	0.16	0.13	0.02	0.04	0.11	0.15	0.11	0.18	0.12	0.12	0.13	0.10	0.15	0.12																
MM	0.03	0.02	0.02	0.05	0.05	0.01	0.02	0.04	0.00	0.00	0.04	0.03	0.01	0.04	0.04	0.06	0.04	0.01	0.04	0.02	0.03															
MU	0.17	0.13	0.15	0.04	0.13	0.12	0.14	0.12	0.05	0.07	0.12	0.13	0.08	0.12	0.12	0.14	0.11	0.10	0.15	0.12	0.11	0.04														
NB	0.18	0.12	0.13	0.05	0.11	0.13	0.14	0.10	0.04	0.07	0.08	0.14	0.09	0.12	0.16	0.17	0.13	0.12	0.13	0.10	0.10	0.04	0.17													
NJ	0.18	0.15	0.19	0.07	0.15	0.15	0.17	0.14	0.03	0.06	0.12	0.19	0.10	0.18	0.08	0.16	0.12	0.13	0.19	0.13	0.15	0.03	0.14	0.11												
NK	0.16	0.16	0.17	0.07	0.15	0.16	0.16	0.14	0.03	0.08	0.12	0.17	0.09	0.13	0.10	0.14	0.12	0.12	0.15	0.14	0.12	0.03	0.13	0.14	0.16											
RD	0.07	0.06	0.04	0.03	0.05	0.05	0.05	0.07	0.03	0.03	0.03	0.07	0.07	0.05	0.07	0.08	0.09	0.05	0.07	0.05	0.07	0.02	0.07	0.08	0.03	0.03										
RH	0.06	0.06	0.07	0.10	0.09	0.07	0.09	0.06	0.04	0.06	0.06	0.08	0.07	0.09	0.08	0.12	0.11	0.07	0.08	0.07	0.10	0.05	0.07	0.09	0.07	0.17	0.04									
SR	0.11	0.10	0.12	0.07	0.11	0.13	0.11	0.10	0.05	0.06	0.10	0.13	0.08	0.13	0.11	0.14	0.11	0.11	0.12	0.10	0.12	0.04	0.10	0.10	0.12	0.13	0.05	0.12								
TK	0.15	0.12	0.14	0.02	0.15	0.12	0.11	0.16	0.01	0.07	0.13	0.13	0.06	0.07	0.07	0.12	0.07	0.08	0.14	0.12	0.08	0.03	0.11	0.08	0.11	0.14	0.08	0.03	0.07							
VN	0.15	0.14	0.16	0.06	0.16	0.13	0.21	0.11	0.04	0.08	0.11	0.15	0.09	0.14	0.11	0.13	0.11	0.13	0.18	0.15	0.10	0.03	0.13	0.14	0.16	0.15	0.04	0.07	0.10	0.11						
VT	0.01	0.02	0.00	0.02	0.01	0.02	0.02	0.04	0.00	0.01	0.02	0.03	0.04	0.03	0.02	0.03	0.03	0.02	0.03	0.01	0.03	0.04	0.01	0.02	0.01	0.00	0.04	0.01	0.03	0.02	0.00					
ZA	0.08	0.09	0.09	0.08	0.10	0.09	0.10	0.06	0.05	0.02	0.06	0.10	0.09	0.10	0.13	0.13	0.11	0.10	0.10	0.06	0.10	0.06	0.09	0.10	0.08	0.09	0.09	0.08	0.10	0.05	0.10	0.07				
ZF	0.13	0.12	0.13	0.08	0.12	0.12	0.12	0.12	0.01	0.05	0.09	0.13	0.05	0.09	0.06	0.10	0.09	0.07	0.13	0.10	0.11	0.03	0.08	0.06	0.11	0.11	0.04	0.06	0.09	0.11	0.09	0.01	0.06			
ZM	0.11	0.12	0.10	0.06	0.09	0.10	0.11	0.09	0.07	0.03	0.07	0.12	0.11	0.09	0.15	0.15	0.16	0.17	0.10	0.09	0.11	0.05	0.10	0.12	0.07	0.09	0.11	0.09	0.10	0.09	0.10	0.05	0.14	0.10		
ZT	0.18	0.15	0.18	0.06	0.14	0.14	0.18	0.15	0.03	0.09	0.14	0.18	0.10	0.16	0.09	0.16	0.12	0.14	0.20	0.17	0.15	0.04	0.13	0.12	0.20	0.15	0.05	0.07	0.12	0.13	0.16	0.02	0.10	0.11	0.13	

APPENDIX E.2

Dyadic Association Indices During Food Rich Period

	AY	BB	BK	BN	BY	CL	DN	GS	HT	EM	JM	JN	KG	KK	KL	KU	KW	KY	MA	MG	MK	MM	MU	NB	NJ	NK	RD	RH	SR	TK	VN	VT	ZA	ZF	ZM	ZT
AY																																				
BB	0.15																																			
BK	0.22	0.16																																		
BN	0.11	0.16	0.09																																	
BY	0.22	0.15	0.22	0.15																																
CL	0.17	0.14	0.17	0.07	0.12																															
DN	0.22	0.16	0.18	0.15	0.20	0.14																														
GS	0.17	0.16	0.19	0.10	0.17	0.09	0.14																													
HT	0.05	0.06	0.07	0.00	0.05	0.09	0.04	0.04																												
EM	0.05	0.07	0.06	0.00	0.09	0.04	0.05	0.06	0.00																											
JM	0.11	0.06	0.13	0.02	0.16	0.11	0.10	0.10	0.05	0.12																										
JN	0.21	0.15	0.18	0.12	0.17	0.15	0.20	0.15	0.01	0.05	0.12																									
KG	0.12	0.15	0.14	0.11	0.10	0.09	0.11	0.10	0.03	0.03	0.05	0.11																								
KK	0.21	0.15	0.22	0.11	0.23	0.14	0.22	0.19	0.03	0.10	0.14	0.20	0.12																							
KL	0.13	0.17	0.15	0.13	0.14	0.13	0.13	0.10	0.16	0.00	0.06	0.12	0.16	0.11																						
KU	0.23	0.16	0.23	0.12	0.21	0.14	0.17	0.17	0.11	0.01	0.12	0.16	0.14	0.19	0.19																					
KW	0.19	0.20	0.17	0.17	0.17	0.15	0.18	0.12	0.09	0.02	0.06	0.16	0.14	0.17	0.20	0.20																				
KY	0.16	0.16	0.15	0.13	0.15	0.14	0.18	0.12	0.03	0.09	0.06	0.17	0.13	0.19	0.14	0.13	0.23																			
MA	0.21	0.14	0.21	0.13	0.20	0.16	0.22	0.16	0.07	0.07	0.11	0.17	0.14	0.20	0.14	0.17	0.19	0.16																		
MG	0.21	0.14	0.21	0.12	0.22	0.14	0.21	0.21	0.05	0.07	0.13	0.17	0.13	0.22	0.15	0.19	0.19	0.13	0.23																	
MK	0.16	0.16	0.18	0.15	0.17	0.11	0.22	0.16	0.07	0.01	0.09	0.19	0.14	0.20	0.16	0.16	0.19	0.12	0.17	0.19																
MM	0.04	0.10	0.05	0.15	0.11	0.01	0.09	0.05	0.00	0.00	0.01	0.06	0.12	0.07	0.12	0.09	0.10	0.07	0.06	0.06	0.11															
MU	0.18	0.13	0.17	0.09	0.19	0.14	0.15	0.15	0.08	0.08	0.14	0.13	0.14	0.18	0.16	0.18	0.19	0.14	0.19	0.15	0.24	0.07														
NB	0.20	0.13	0.15	0.13	0.17	0.15	0.19	0.10	0.07	0.04	0.07	0.14	0.14	0.15	0.19	0.19	0.20	0.15	0.17	0.14	0.12	0.08	0.19													
NJ	0.21	0.16	0.21	0.14	0.20	0.13	0.21	0.18	0.03	0.08	0.11	0.20	0.11	0.24	0.11	0.21	0.21	0.18	0.19	0.19	0.21	0.08	0.16	0.14												
NK	0.20	0.21	0.20	0.13	0.17	0.16	0.18	0.17	0.06	0.08	0.12	0.20	0.15	0.19	0.15	0.22	0.24	0.18	0.17	0.19	0.16	0.05	0.16	0.15	0.21											
RD	0.08	0.08	0.06	0.04	0.06	0.13	0.05	0.04	0.08	0.00	0.00	0.00	0.10	0.03	0.10	0.07	0.09	0.02	0.08	0.09	0.04	0.00	0.08	0.07	0.00	0.05										
RH	0.14	0.15	0.15	0.14	0.12	0.11	0.17	0.10	0.08	0.04	0.06	0.13	0.13	0.13	0.18	0.19	0.22	0.12	0.14	0.13	0.31	0.10	0.14	0.17	0.15	0.21	0.05									
SR	0.17	0.17	0.17	0.14	0.17	0.13	0.16	0.15	0.03	0.08	0.11	0.17	0.14	0.20	0.15	0.15	0.21	0.16	0.16	0.20	0.24	0.08	0.15	0.14	0.20	0.19	0.04	0.29								
TK	0.15	0.12	0.15	0.02	0.17	0.16	0.10	0.14	0.04	0.10	0.11	0.11	0.07	0.11	0.09	0.12	0.10	0.14	0.14	0.14	0.04	0.01	0.13	0.09	0.11	0.12	0.10	0.06	0.10							
VN	0.13	0.12	0.15	0.15	0.19	0.12	0.19	0.11	0.00	0.10	0.11	0.15	0.16	0.20	0.12	0.14	0.15	0.18	0.15	0.17	0.17	0.11	0.13	0.15	0.18	0.17	0.01	0.26	0.16	0.09						
VT	0.00	0.03	0.00	0.06	0.02	0.01	0.01	0.05	0.00	0.00	0.00	0.02	0.05	0.02	0.03	0.01	0.02	0.01	0.01	0.01	0.04	0.07	0.02	0.02	0.03	0.01	0.00	0.02	0.01	0.02	0.02					
ZA	0.13	0.14	0.14	0.17	0.18	0.11	0.13	0.07	0.09	0.01	0.09	0.15	0.16	0.11	0.18	0.19	0.23	0.13	0.16	0.11	0.30	0.17	0.18	0.17	0.12	0.13	0.08	0.23	0.11	0.10	0.15	0.03				
ZF	0.10	0.11	0.08	0.14	0.10	0.11	0.11	0.08	0.01	0.00	0.07	0.13	0.07	0.11	0.07	0.07	0.12	0.10	0.12	0.10	0.19	0.04	0.08	0.05	0.10	0.09	0.00	0.10	0.11	0.07	0.09	0.03	0.11			
ZM	0.13	0.17	0.13	0.16	0.15	0.14	0.13	0.09	0.14	0.03	0.05	0.10	0.12	0.11	0.16	0.15	0.22	0.14	0.13	0.12	0.19	0.12	0.13	0.13	0.11	0.13	0.08	0.26	0.12	0.10	0.13	0.01	0.18	0.09		
ZT	0.20	0.15	0.22	0.14	0.21	0.13	0.20	0.18	0.01	0.11	0.13	0.20	0.12	0.22	0.09	0.18	0.15	0.17	0.21	0.22	0.23	0.07	0.14	0.12	0.23	0.18	0.02	0.27	0.16	0.16	0.19	0.02	0.11	0.10	0.10	

APPENDIX E.3

Dyadic Association Indices During Food Poor Period

	AY	BB	BK	BN	BY	CL	DN	GS	HT	EM	JM	JN	KG	KK	KL	KU	KW	KY	MA	MG	MK	MM	MU	NB	NJ	NK	RD	RH	SR	TK	VN	VT	ZA	ZF	ZM	ZT
AY																																				
BB	0.13																																			
BK	0.19	0.12																																		
BN	0.03	0.00	0.00																																	
BY	0.10	0.05	0.14	0.00																																
CL	0.10	0.04	0.11	0.08	0.01																															
DN	0.12	0.08	0.17	0.00	0.11	0.15																														
GS	0.15	0.11	0.02	0.05	0.05	0.13	0.04																													
HT	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00																												
EM	0.17	0.04	0.16	0.06	0.14	0.12	0.06	0.13	0.00																											
JM	0.18	0.06	0.17	0.00	0.02	0.10	0.03	0.06	0.00	0.11																										
JN	0.13	0.10	0.12	0.05	0.00	0.20	0.12	0.11	0.00	0.10	0.13																									
KG	0.03	0.08	0.00	0.00	0.00	0.05	0.01	0.05	0.00	0.07	0.00	0.07																								
KK	0.10	0.03	0.02	0.12	0.02	0.13	0.01	0.14	0.00	0.09	0.06	0.09	0.08																							
KL	0.15	0.18	0.12	0.04	0.08	0.08	0.13	0.13	0.00	0.11	0.04	0.11	0.07	0.05																						
KU	0.10	0.08	0.08	0.05	0.03	0.18	0.09	0.15	0.00	0.06	0.08	0.17	0.08	0.16	0.08																					
KW	0.13	0.20	0.11	0.05	0.09	0.07	0.13	0.07	0.00	0.07	0.03	0.13	0.05	0.05	0.23	0.11																				
KY	0.11	0.17	0.12	0.00	0.03	0.01	0.10	0.01	0.00	0.02	0.05	0.06	0.01	0.03	0.13	0.04	0.18																			
MA	0.12	0.09	0.11	0.00	0.06	0.19	0.19	0.09	0.00	0.07	0.07	0.12	0.07	0.10	0.05	0.17	0.04	0.03																		
MG	0.13	0.15	0.13	0.00	0.08	0.09	0.16	0.10	0.00	0.06	0.07	0.05	0.01	0.06	0.08	0.14	0.09	0.06	0.16																	
MK	0.03	0.05	0.00	0.10	0.00	0.05	0.07	0.04	0.00	0.05	0.00	0.03	0.08	0.07	0.03	0.03	0.07	0.06	0.04	0.03																
MM	0.04	0.02	0.04	0.14	0.00	0.07	0.00	0.04	0.00	0.00	0.08	0.09	0.00	0.07	0.07	0.09	0.08	0.00	0.00	0.00	0.00															
MU	0.16	0.08	0.20	0.00	0.06	0.15	0.16	0.06	0.00	0.12	0.17	0.15	0.00	0.12	0.10	0.09	0.11	0.07	0.12	0.13	0.01	0.04														
NB	0.22	0.14	0.16	0.04	0.04	0.17	0.13	0.12	0.00	0.14	0.14	0.20	0.04	0.12	0.17	0.14	0.17	0.10	0.12	0.11	0.00	0.09	0.19													
NJ	0.07	0.03	0.05	0.00	0.02	0.15	0.10	0.06	0.00	0.02	0.09	0.10	0.00	0.11	0.02	0.12	0.03	0.06	0.14	0.09	0.02	0.00	0.08	0.06												
NK	0.15	0.12	0.19	0.07	0.05	0.12	0.10	0.08	0.00	0.10	0.14	0.13	0.00	0.06	0.13	0.06	0.11	0.10	0.03	0.08	0.00	0.15	0.15	0.18	0.03											
RD	0.08	0.05	0.06	0.15	0.03	0.06	0.00	0.11	0.00	0.12	0.04	0.03	0.03	0.14	0.09	0.04	0.07	0.05	0.00	0.04	0.08	0.08	0.03	0.07	0.00	0.05										
RH	0.04	0.05	0.00	0.17	0.03	0.13	0.01	0.10	0.00	0.07	0.02	0.12	0.13	0.15	0.10	0.13	0.08	0.00	0.07	0.00	0.00	0.18	0.00	0.11	0.00	0.14	0.09									
SR	0.01	0.01	0.02	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.05	0.00	0.01	0.03	0.02	0.00	0.00								
TK	0.12	0.07	0.04	0.00	0.06	0.05	0.05	0.23	0.00	0.04	0.08	0.06	0.00	0.11	0.05	0.07	0.01	0.01	0.07	0.06	0.00	0.00	0.06	0.08	0.05	0.09	0.00	0.02	0.00							
VN	0.12	0.14	0.15	0.00	0.09	0.16	0.25	0.05	0.00	0.09	0.03	0.15	0.04	0.08	0.13	0.10	0.14	0.13	0.16	0.12	0.06	0.00	0.14	0.13	0.11	0.07	0.00	0.04	0.00	0.04						
VT	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
ZA	0.15	0.13	0.20	0.00	0.13	0.01	0.13	0.00	0.00	0.09	0.06	0.04	0.00	0.00	0.16	0.04	0.17	0.19	0.00	0.07	0.00	0.00	0.09	0.11	0.02	0.14	0.09	0.00	0.00	0.00	0.11	0.00				
ZF	0.10	0.14	0.09	0.10	0.08	0.10	0.07	0.12	0.00	0.07	0.06	0.09	0.01	0.06	0.13	0.14	0.15	0.14	0.04	0.07	0.07	0.06	0.02	0.07	0.07	0.08	0.12	0.07	0.00	0.03	0.07	0.00	0.15			
ZM	0.15	0.19	0.14	0.03	0.07	0.04	0.12	0.10	0.00	0.07	0.07	0.10	0.01	0.03	0.21	0.10	0.22	0.23	0.01	0.12	0.05	0.06	0.10	0.15	0.03	0.12	0.10	0.05	0.00	0.05	0.13	0.00	0.20	0.17		
ZT	0.20	0.17	0.17	0.00	0.05	0.08	0.12	0.10	0.00	0.06	0.14	0.09	0.06	0.14	0.12	0.12	0.14	0.15	0.14	0.12	0.01	0.08	0.15	0.16	0.07	0.16	0.07	0.08	0.03	0.08	0.12	0.00	0.15	0.09	0.14	

APPENDIX F

Death of a wild chimpanzee community member: Possible outcome of intense sexual competition.

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Katie Fawcett[1] and Geresomu Muhumuza[2]

[1]Scottish Primate Research Group, Institute of Cell, Animal and Population Biology, Edinburgh University, Kings Buildings, West Mains Road, Edinburgh, EH9 3JT, UK.

[2]Budongo Forest Project, PO Box 362, Masindi, Uganda.

RUNNING HEAD: Death of a wild chimpanzee community member.

Corresponding author:
Katie Fawcett
Institute of Cell, Animal and Population Biology
Edinburgh University
Kings Buildings
West Mains Road
Edinburgh
EH9 3JT, UK.
Tel. 00 44 131 6505510
Katie.Fawcett@ed.ac.uk

ABSTRACT

Our observations strongly support the view that a lethal gang attack occurred against a young adult male within a wild chimpanzee (*Pan troglodytes schweinfurthii*) community. This is the first report of such an occurrence. At least three adult male chimpanzees are believed to have been involved in the attack. This case is unusual because the attack was fatal, involved directed group aggression within a community and was not linked to the overthrow of the alpha male. During the period before the attack the percentage of cycling females in the community was very low (15 males : 17 females, a maximum of 2 regularly cycling). This fact, coupled with the presence of one female in full genital tumescence, may have incited and escalated the violence of the attack. The lethal attack is interpreted as an act of intra-community male sexual competition resulting in the complete exclusion of one male from estrous females.

KEY WORDS Chimpanzee; *Pan troglodytes schweinfurthii*; Budongo; Aggression

INTRODUCTION

The lethal aggressive behavior of chimpanzees, although rare, is now believed to occur in several study sites across Africa [Nishida et al., 1985; Goodall 1986; Wrangham & Peterson, 1996]. Lethal aggression may occur both between and within chimpanzee communities and involve attacks targeted at both adult and infant chimpanzees [Bygott, 1972; Goodall, 1986; Nishida, 1990, 1996; Newton-Fisher, 1999a]. However, violent gang aggression involving adult chimpanzees of the same community is not common [Goodall, 1992]. To date there has been only one event which has resulted in the death of the victim in a wild community [Nishida, 1996] and another in captivity [de Waal, 1982, 1986]. Both of these events centered around the overthrow of an alpha male. The case reported here describes the occurrence of lethal aggression within a wild community at a non-provisioned site and differs from previous incidences by the fact that the targeted male was not the alpha male. It provides evidence that the usual tension reducing mechanism of social dominance may break down with fatal consequences, even without the extreme contest situation for alpha status.

METHODS

Observations were made during an on-going field study of the behavior of the Sonso chimpanzee community, Budongo Forest, Uganda. Prof. V. Reynolds and a team of research assistants and students have been observing and collecting behavioral and ecological data from this community since 1990 [Reynolds, 1992]. On the date of the attack, the community consisted of 54 individuals. The attack is presumed to have been initiated at 0640hrs when calls were first heard from camp. Direct behavioral observations of the attack began when the chimpanzees were located at 0720hrs. Ad lib sampling methods were used to record all details of the event. Following the attack, a total of 5 field assistants and three students were in the field in order to locate and to document the behavior of as many community members as possible. The motive for this attack is discussed in light of the available evidence.

RESULTS

At 0640 hours on 4 November 1998, fear screams or "wraa" calls [Goodall, 1986] were heard SE of camp. The chimpanzees were located by 0720 hours, within the core area of the community home range. Wraa calls were still being emitted.Visibility was poor due to the low lighting conditions and dense undergrowth. There was a flattened area of vegetation approximately 5-7m^2 and an adult male chimpanzee lying in a prone position, tentatively identified as *Zesta*. At approximately 0730 *Magosi*, an old adult male (ex-alpha), charged at and then circled *Zesta*. He was followed shortly afterwards by *Black*, another prime adult male (gamma rank [Newton-Fisher, 1997]). *Black*, whilst displaying, ran at *Zesta*, leapt on his body, then violently and repeatedly shook *Zesta*. Throughout this *Zesta* was screaming. Another unidentified prime adult male was also observed displaying on the ground around *Zesta*. We retreated to the edge of the group of chimpanzees, approximately 10m from *Zesta*. At 0840, the chimpanzees were now quiet and beginning to disperse, we were able to approach *Zesta* and obtain a positive identification. His breathing was labored and shallow and he died shortly afterwards. Most of the other community members had now left. *Ruda*, an adult female, with her infant and juvenile son and *Sara*, a sub-adult female remained. They approached *Zesta*. *Sara* 'whimpered' [Goodall, 1986] as she gently shook and pulled *Zesta*. By 1030 *Zesta* was left alone. In total we observed 6 adult males, 1 adult female and infant, 2 sub-adult males, 4 sub-adult females and 2 juvenile males at the scene of the incident (not including *Zesta*). Of these, *Janie*, a late sub-adult female, was observed to be present in maximal tumescence. By the time of nesting all community males had been seen. *Duane*, the alpha male, *Andy*, a sub-adult male, and *Black* were all observed to have sustained superficial injuries. A fecal sample collected from *Duane* during the afternoon of the attack was found to contain pieces of flesh, thus further implicating his involvement in the attack, (fecal samples were not collected from other individuals). The flesh (approx. 2cm^2) was identified as that of a chimpanzee by the hairs attached. We suggest that due to the nature of *Zesta's* wounds, the swallowing of flesh was probably accidental, rather than intended cannibalism. Two sections of muscle (4cm^2 and 2cm^2) were also found in the flattened area where the fight had occurred.

A post-mortem superficial examination and palpation of *Zesta* were carried out during the afternoon of the attack by a qualified veterinarian. It was concluded that death had resulted from a pneumothorax caused by a penetrating injury to the right thorax. Severe blood loss from the multiple extensive injuries sustained, particularly to the right upper arm and left lower leg would have contributed to the rapid onset of death. Internal organ damage was also expected. It appeared from the extent and severity of the injuries that several chimpanzees were involved during the attack. The size and shape of the wounds were not considered to be characteristic of an attack by a leopard. In addition, leopards are not thought to be present in the study area. A minimally invasive examination was made in order to ensure that the body was left undisturbed. It was suspected that the continuing presence of the body would be important over the following days for the adjustment of community members. Indeed the following day *Ruda* and family returned to *Zesta* briefly. DNA analyses are not available in order to evaluate kinship relationships in this community.

Observations from the previous day recorded no unusual behavior in the community. *Zesta* was not observed to be ill or the target of aggression. The time of the attack would have coincided with the usual waking up time of the chimpanzees. Thus there appears to have been no substantial period of build up to the attack on that day.

DISCUSSION

The results of the post-mortem examination support the notion that death was the result of an attack by a group of chimpanzees. Such observations as were made suggest that this attack was by members of the same community as the victim. This is further supported by the fact that the attack occurred within the core of the community home range area.

Zesta was the youngest and lowest ranking of all adult males in the community. It appears unlikely that this death can be interpreted as the outcome of a political power struggle for alpha position. Generally, intense rivalry occurs predominantly between the top ranking males [Riss & Goodall, 1977; de Waal, 1982, 1986; Nishida, 1983; Newton-Fisher, 1997]. It is unclear how the death of *Zesta* could result in the strengthening of the rank position of any of the other males. The main situations under which competition between males may occur are: within group feeding and mating competition; between group mating and feeding competition; and the protection of offspring [van Hooff and van Schaik, 1991; Daly and Wilson, 1994]. In the cases of between group feeding and mating competition and the protection of offspring, males can be expected to co-operate. However, in the cases of within group feeding and mating competition, if possible, a male may attempt to exclude other group members [van Hooff and van Schaik, 1991]. This event did not occur during a month of food scarcity, therefore the event is considered to be a result of mating competition.

At the time of the attack there was one late sub-adult female, *Janie*, in maximal tumescence. This fact alone would not offer a sufficient explanation for such intense sexual competition. During a previous study at Budongo 35% of parties were found to have only one female exhibiting maximal tumescence [Newton-Fisher, 1999b]. However, at the time of the attack there was an unusual sex ratio of mature individuals in the community (0.94, 15 males:17 females). Generally, the ratio of male to female individuals in a chimpanzee community is biased towards an increased number of females, (i.e. 0.66 (Kibale Forest) & 0.25 (Tai Forest) [Boesch, 1996]). Before the Gombe community split in 1970 [Goodall, 1986], the number of sexual partners available to males was very low. The need to recruit young cycling females into the community may have influenced the ranging patterns and extreme aggressive behavior, of the males at that time [Goodall, 1986a]. In the case reported here from Budongo, the situation of an unusual adult sex ratio was further magnified by the fact that all of the adult females except one, *Mama*, who was old and very rarely observed, had infants at the time of the attack and were not exhibiting any swelling cycles. Of the remaining six sub-adult females, three had not yet started regular cycles and another two were suspected to be pregnant and exhibiting irregular swellings, which were of no interest to the males. This may have resulted in intense mating competition for access to *Janie*. From previous ad lib records of copulation

events, *Zesta* was the most frequent copulation and grooming partner of *Janie* [copulations 18, N=96; grooming 6, N=25; Fawcett, unpublished data]. It is hypothesized that a preferential relationship between *Zesta* and *Janie*, and the presence of *Janie* in maximal tumescence, may have both instigated and escalated the violence of the attack. We suggest that *Zesta*, a young adult male, may not have observed his position within the male hierarchy, and thus became the target of aggression. At Mahale, the ostracism of a young adult male was also interpreted to be a result of inappropriate social behavior [Nishida et al.1995]. In captivity, Alford et al. [1995] observed, significant increases in the level of wounding when one or more females at maximal genital tumescence were present in the group and that serious, even life threatening wounding may result from the introduction of younger, relatively socially inexperienced males to older socially experienced males. This case provides evidence that the lethal aggressive behavior of adult chimpanzees observed between gangs from different communities can also occur within a wild, non-provisioned chimpanzee community.

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